

VOLE POPULATION FLUCTUATIONS: FACTORS THAT INITIATE AND DETERMINE INTERVALS BETWEEN THEM IN *MICROTUS OCHROGASTER*

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We studied factors associated with occurrence of high-amplitude population fluctuations of the prairie vole (*Microtus ochrogaster*) in alfalfa, bluegrass, and tallgrass habitats in east-central Illinois for 25 years. Increased survival was the most important factor associated with initiation of a population fluctuation during a given year. The proportion of reproductively active adult females was not associated with initiation of population fluctuations. The interval between fluctuations was not correlated with the previous peak density. We propose that population fluctuations in *M. ochrogaster* were initiated by the net effects of relaxation of predation pressure of multiple generalist predators, which occurred erratically across years.

Key words: *Microtus ochrogaster*, population cycles, population fluctuations, prairie vole, survival

Populations of most arvicoline rodents undergo large-scale fluctuations in numbers. Some population fluctuations are short-term, occurring 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 may be annual or erratic, or fluctuations may occur at 2- to 5-year intervals, in which case they are described as population “cycles” (Bjørnstad et al. 1998; Krebs 1996; Krebs et al. 1969; Krebs and Myers 1974; Taitt and Krebs 1985; Turchin 2003).

Survival and reproduction are presumed to be the primary demographic variables responsible for temporal and spatial differences in demography of arvicoline rodents (Batzli 1992, 1996; Krebs and Myers 1974; Lin and Batzli 2001), whereas emigration and immigration do not appear to be important factors influencing population fluctuations (Dueser et al. 1981; Gaines and McClenaghan 1980; Getz et al. 2005a; Lin and Batzli 2001; Verner and Getz 1985). Explanations of what initiates a population increase can be grouped into hypotheses that are survival based (greater survival during the winter preceding a fluctuation [in eastern North America] and during the increase) and reproduction based (high levels of reproduction

the winter preceding a fluctuation, earlier than normal beginning of reproduction, greater reproduction during the increase, and earlier age of 1st reproduction—Batzli 1992; Boonstra et al. 1998; Gaines and Rose 1976; Krebs et al. 1969; Krebs and Myers 1974; Oli and Dobson 1999; Pinter 1988).

Hypotheses explaining the effects of peak densities on the interval until the next population fluctuation are delayed density-dependent effects of high densities on condition of the voles (Christian 1971, 1980; Norrdahl and Korpimäki 2002a); delayed density-dependent recovery of the habitat from effects of the previous high densities (Agrell et al. 1995; Batzli 1992); and delayed density-dependent predator–prey effects on mortality of the voles (Klemola et al. 2000; Korpimäki and Norrdahl 1991).

During the course of a 25-year study of demography of the prairie vole (*Microtus ochrogaster*—Getz et al. 2001), we collected data relevant to questions concerning conditions that initiate fluctuations and determine length of interval between population fluctuations. Data were obtained from 3 habitats in which there were a total of 30 population fluctuations of *M. ochrogaster*. Getz et al. (2001) concluded that the population fluctuations of *M. ochrogaster* in these study sites were cyclic in nature, whereas more comprehensive analysis (Turchin 2003) indicated that the populations fluctuated erratically. Regardless of the pattern of fluctuation, our study populations exhibited large-scale fluctuations in abundance, and our goal is to explain the demographic causes of these fluctuations.

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We tested survival-based and reproductive-based hypotheses by comparing the following for years with and without population fluctuations: survival in the preceding winter; survival during the typical period of population increase (summer–autumn); reproduction in the preceding winter; and reproduction during the typical period of population increase. We also compared survival and reproduction during the increase phase (the period of population growth to the peak) against these traits in the preceding low-density trough phase for years in which there was a population fluctuation. Finally, we tested the hypothesis that there is a correlation between peak density of a population fluctuation and the interval until the next fluctuation.

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 northeast of Urbana, Illinois (40°15′N, 88°28′W). We monitored populations of *M. ochrogaster* from May 1972 to May 1997 in 0.5–2.0 ha of restored tallgrass prairie (a mixture of big bluestem [*Andropogon gerardii*], Indian grass [*Sorghastrum nutans*], and switch grass [*Panicum*]) sites, in 1.0–2.0 ha of bluegrass (*Poa pratensis*) sites, and in 1.0–1.4 ha of alfalfa (*Medicago sativa*) sites. These sites are described elsewhere (Getz et al. 1979, 1987, 2001) and were located within a radius of 500 m and were surrounded by cultivated fields, a 29-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 study sites either had boundaries of unsuitable vole habitat or the adjacent site also was trapped, allowing for accounting of individuals whose home ranges extended into an adjacent site (Getz et al. 2001). Other widely dispersed vole habitat within the region consisted of approximately 2-m-wide mown county roadsides, approximately 5-m-wide banks of drainage ditches, <0.25-ha uncultivated sites, and 4- to 5-m-wide margins of an interstate highway 0.75 km from the study area.

Trapping Procedures

We established a grid system with 10-m intervals in all study sites, and placed 1 locally made wooden multiple-capture live trap (Burt 1940) at each station. Each month we prebaited traps for 2 days and then trapped for 3 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 3 days. At 1st 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 (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 lactating), and body mass to the nearest 1 g. For analysis, we considered animals that weighed ≤ 29 g as young and those weighing ≥ 30 g as adult (Fitch 1957; Gier and Cooksey 1967; Hasler 1975).

Data Analysis

Population fluctuations.—Demographic data used in the analyses are from Getz et al. (2001), who employed the minimum number known to be alive model (Krebs 1999) to estimate population densities and survival. Capture–mark–recapture analysis (Lebreton et al. 1992)

also has been employed to estimate density and survival; however, estimates of population density and survival for periods of low densities (< 10 voles/ha), which constituted about one-third of the months of the study, were either not possible or obviously unreliable (G. Hryciyshyn, pers. comm.). Because survival during periods of low density is essential for testing the proposed hypotheses, we used the estimates of minimum number alive. Trappability in our study was high, estimated to be approximately 92%, in part because of use of multiple-capture live traps.

We defined individual population fluctuations as those with peaks exceeding the following densities: alfalfa, 75 voles/ha; bluegrass, 25 voles/ha; and tallgrass, 20 voles/ha. These fluctuations stood out as conspicuous events that were more than twice the highest densities of nonfluctuation years in each habitat (alfalfa, peak densities 2.4 times greater than the mean high density for years without fluctuations, 30.4 ± 8.1 voles/ha; bluegrass, 4.0 times the mean high density of nonfluctuation years, 6.2 ± 1.9 voles/ha; and tallgrass, 3.7 times the mean nonfluctuation year high density, 5.4 ± 1.5 voles/ha). The peak densities were somewhat lower than those reported by Taitt and Krebs (1985) from published short-term studies; perhaps only unusually high-density fluctuations have been used as the basis of publications. Differences in peak densities among the 3 habitats reflected differences in habitat quality (Getz et al. 2005b).

All fluctuations except 1 were ≤ 1 year in duration. The mean ($\pm SE$) time from onset of the increase to peak density was 4.3 ± 0.4 months; the mean duration of a complete fluctuation, from beginning of the increase to the end of the decline, was 8.3 ± 0.6 months. Thus, we were able to categorize calendar years during which a population fluctuation occurred or did not occur. For seasonal analyses we allocated all observations to spring (March–May), summer (June–August), autumn (September–November), or winter (December–February). The increase phase of 22 of the 30 population fluctuations began in summer or autumn; 26 fluctuations peaked in autumn or winter (Getz et al. 2001).

We examined survival as the proportion of animals present in 1 month that survived to the next month and persistence of voles 1st captured as young and presumed to have been born on the study site. We assumed voles recorded as young in a given trapping session were born midway between that trapping session and the previous session. Voles that disappeared from a site were presumed to have done so midway between the last session in which they were captured and the subsequent session. Thus, young voles captured in only 1 month were given a persistence of 1 month. Because of small sample sizes, we combined persistence data for young males and females. Here, survival (including persistence of young) includes both in situ mortality and emigration; the former is presumed to be the most prevalent cause of disappearance (Verner and Getz 1985). Because reproductive condition of females can be determined more accurately than can that of males, for our analyses of effects of reproduction we used the proportion of the adult females that were reproductively active (vagina open, pregnant, or lactating) as an index of reproductive activity of the population.

Interval between population fluctuations.—Length of time until the next population fluctuation may result from adverse effects of population density on habitat quality or condition of the animals, and a resultant lag-time for recovery. We therefore compared peak density of a population fluctuation with length of the decline phase, rate of the decline, population density during the subsequent trough density, and length of time until the next population fluctuation.

Statistical Analyses

We used general linear models (analysis of covariance; SAS procedure GLM [SAS Institute Inc. 1999]) to investigate the effects of

season, population density, and population fluctuations on survival and proportion of reproductively active adult females. Specifically, we asked whether survival (or proportion of adult females that were reproductively active) in each habitat differed between fluctuation and nonfluctuation years, after accounting for seasonal variation and effects of population density. Survival and reproductive data were arcsine square-root transformed (Zar 1999). We 1st fitted a model with all main effects, and all 2-way and 3-way interactions. Then, we sequentially removed nonsignificant ($\alpha = 0.05$) interaction effects, starting with the highest interaction term with the largest *P*-value. We refitted the model, removed another highest-order interaction term with the largest *P*-value, and repeated the process until all nonsignificant interaction terms were removed (e.g., Slade et al. 1997). The final general linear model contained main effects and significant interaction effects. Using the final model we estimated least-squares means (LSMs) for each significant interaction term involving categorical variables and tested for differences in least-squares means using Bonferroni adjustments. Because population density is a continuous variable, 2-way interaction effects involving density were further examined using linear regression analysis for each level of the categorical variable involved in the interaction.

There were too few data from tallgrass for general linear models analysis. Sample sizes of young and adult survival rates and persistence of young on the study sites from all 3 habitats were inadequate for analyses involving these variables within the general linear models framework. We used 2-sample *t*-tests to compare persistence of young between years with and without population fluctuations and for comparisons of all variables between the increase and trough phases of years with population fluctuations. We used partial correlation analysis to test for the effect of peak densities on time until the next population fluctuation.

Because most of the variables did not meet the requirements for normality (population densities and demographic variables were nonnormal at the 0.05 level; Kolmogorov–Smirnov test [Zar 1999]), all variables were log-transformed for *t*-test and correlation analyses. For variables that included “zeros,” we added 0.001 before transformation. This allowed us to test for differences using independent-sample *t*-tests, and to assess associations between variables using Pearson’s correlation analyses. When *df.* values 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 1 decimal place. We used SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for these statistical analyses.

All original capture data and explanatory files are available to anyone wishing to make use of them at <http://www.life.uiuc.edu/getz/>.

RESULTS

Population Fluctuations

In alfalfa, none of the variables included in the model significantly influenced total survival (Table 1). However, there was a significant season \times fluctuation interaction indicating that survival across seasons did not change similarly in fluctuation and nonfluctuation years. Specifically, survival was similar in winter regardless of year, but increased in summer and autumn of years with a fluctuation and decreased in summer and autumn of years without a fluctuation (LSM = 0.900 ± 0.094 and 0.715 ± 0.48 , respectively; $P = 0.03$; Table 1; Fig. 1). In bluegrass, total survival was greater during winter and summer and autumn of years of population fluctuations than nonfluctuation years (Table 1; Fig. 1). Density significantly influenced total

TABLE 1.—Results of the analysis of covariance, examining the effects of population density, season, and year with and without a population fluctuation (fluctuation) on survival and proportion of reproductively active adult female *Microtus ochrogaster*. See text for definition of sources. All general linear models were significant (survival: alfalfa, $F = 4.04$, $df. = 4$, 201, $P < 0.01$; bluegrass, $F = 8.60$, $df. = 4$, 164, $P < 0.01$; reproduction: alfalfa, $F = 56.65$, $df. = 3$, 180, $P < 0.01$; bluegrass, $F = 14.05$, $df. = 4$, 134, $P < 0.01$).

Source and habitat	<i>df.</i>	<i>F</i>	<i>P</i>
Survival			
Alfalfa			
Density	1	2.33	0.13
Fluctuation	1	1.54	0.22
Season	1	0.02	0.88
Fluctuation \times season	1	5.09	0.02
Bluegrass			
Density	1	22.55	<0.01
Fluctuation	1	4.66	0.03
Season	1	0.15	0.70
Density \times fluctuation	1	13.33	<0.01
Reproduction			
Alfalfa			
Density	1	1.50	0.22
Fluctuation	1	0.51	0.48
Season	1	163.12	<0.01
Bluegrass			
Density	1	1.59	0.21
Fluctuation	1	7.67	<0.01
Season	1	23.77	<0.01
Fluctuation \times season	1	4.14	0.04

survival both in years with and without population fluctuations in bluegrass (fluctuation years: intercept = 0.604, slope = 0.004, $r^2 = 0.156$, $P < 0.01$; nonfluctuation years: intercept = 0.419, slope = 0.026, $r^2 = 0.143$, $P < 0.01$).

Mean persistence (months \pm SE) of young born during summer and autumn was greater in both alfalfa and bluegrass during years with a population fluctuation than years without a fluctuation (alfalfa: 2.2 ± 0.1 and 1.7 ± 0.1 months, respectively; $t = 3.733$, $df. = 225.2$, $P = 0.01$; bluegrass: 2.1 ± 0.1 and 1.7 ± 0.1 months, respectively; $t = 2.997$, $df. = 119.2$, $P < 0.01$). In alfalfa, the proportion of reproductively active adult females was significantly less during winter than summer and autumn irrespective of whether there was a population fluctuation (Table 1; Fig. 2). In bluegrass, a significantly smaller proportion of adult females was reproductively active during winters preceding years with than years without population fluctuations (LSM = 0.699 ± 0.076 and 1.110 ± 0.118 , respectively; $P = 0.03$). The proportion of reproductively active adult females during summer and autumn did not differ between years with and without population fluctuations in either habitat (Fig. 2).

Survival (total population, adult, and young) and persistence of young on the study site were significantly greater during the increase phase than the preceding trough phase in all 3 habitats (Table 2). The proportion of adult females that

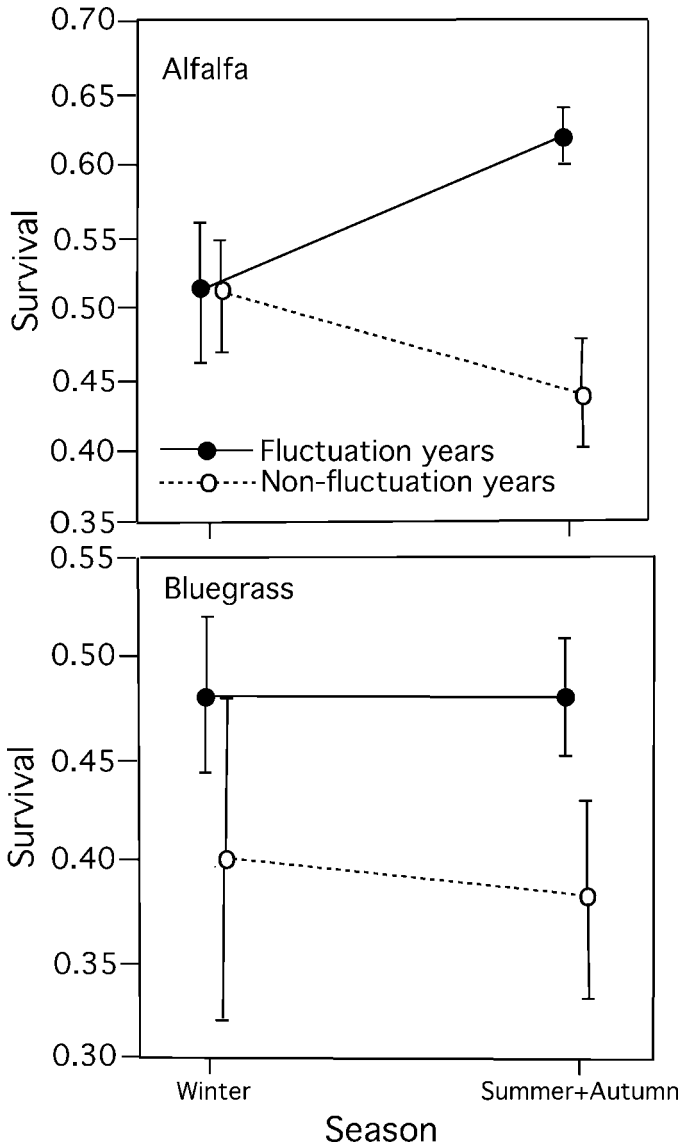


FIG. 1.—Mean (\pm SE) monthly total survival (proportion present surviving until the next month) of *Microtus ochrogaster* during the preceding winter (December–February) and summer + autumn (June–November) of years and when there was and was not a population fluctuation in alfalfa and bluegrass habitats.

was reproductively active did not differ between the trough and subsequent increase phases in alfalfa and bluegrass, whereas significantly fewer adult females were reproductive during the increase versus the previous trough in tallgrass (Table 2).

Intervals Between Population Fluctuations

Peak density of population fluctuations was not significantly correlated with length of the subsequent decline (alfalfa: $r = 0.40$, $P = 0.25$; bluegrass: $r = 0.34$, $P = 0.40$), or with rate of the decline (alfalfa: $r = 0.40$, $P = 0.25$; bluegrass: $r = 0.08$, $P = 0.86$). Mean population density during the trough was not correlated with prior peak density of a population fluctuation (alfalfa: $r = 0.31$, $P = 0.35$; bluegrass: $r = 0.45$, $P = 0.22$), nor

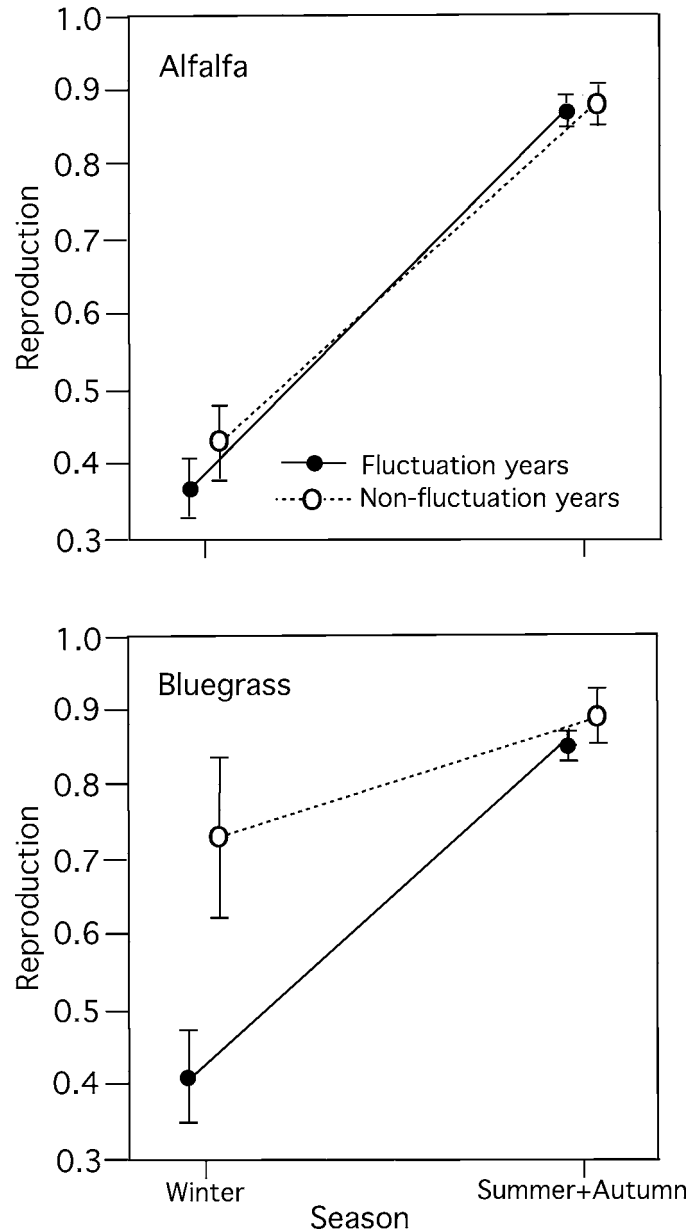


FIG. 2.—Mean (\pm SE) proportion of adult female *Microtus ochrogaster* that were reproductively active (“Reproduction”) during the preceding winter (December–February) and summer + autumn (June–November) of years and when there was and was not a population fluctuation.

was length of the subsequent trough correlated with peak density (alfalfa: $r = -0.55$, $P = 0.08$; bluegrass: $r = 0.23$, $P = 0.60$). Population fluctuations in tallgrass were too few to test characteristics of the decline and subsequent trough phase in relation to prior peak densities. One of the 2 highest peak densities (80 voles/ha) in tallgrass was followed by a trough phase of only 18 months, whereas the other very high peak (92 voles/ha) was followed by a trough of at least 85 months (continued through the end of the study). Lower peak densities (24, 40, and 44 voles/ha) were followed by trough phases of 110, 17, and 17 months, respectively.

TABLE 2.—Comparison of demographic variables during the trough and the subsequent increase phase of *Microtus ochrogaster* population fluctuations. Survival: proportion (mean \pm SE) of individuals surviving to next month. Persistence: number of months (mean \pm SE) individuals 1st captured as young animals remained on the study site. Reproductive: proportion (mean \pm SE) of adult females that were reproductively active each month. Sample sizes are given in parentheses; sample sizes for persistence data are total number of individuals, for other variables, sample sizes are number of months of data included in each sample. Two-sample *t*-tests were used to test for differences in each variable between trough and increase phase. Values with a single asterisk (*) indicate significant difference at $P < 0.01$; those with double asterisks (**) indicate significant difference at $P < 0.001$.

Variable	Alfalfa		Bluegrass		Tallgrass	
	Trough	Increase	Trough	Increase	Trough	Increase
Survival						
Total	0.513 \pm 0.025** (147)	0.686 \pm 0.016** (65)	0.387 \pm 0.030** (128)	0.594 \pm 0.025** (48)	0.309 \pm 0.034** (83)	0.612 \pm 0.038** (20)
Adults	0.445 \pm 0.028** (132)	0.638 \pm 0.018** (67)	0.428 \pm 0.036** (90)	0.571 \pm 0.029** (47)	0.485 \pm 0.046** (40)	0.596 \pm 0.045** (14)
Young	0.235 \pm 0.033** (82)	0.538 \pm 0.030** (62)	0.199 \pm 0.034** (64)	0.384 \pm 0.044** (39)	0.253 \pm 0.060** (34)	0.616 \pm 0.118** (8)
Persistence	1.96 \pm 0.08* (479)	2.15 \pm 0.05* (1529)	1.66 \pm 0.10** (183)	2.19 \pm 0.06** (744)	1.43 \pm 0.10** (122)	2.34 \pm 0.21** (92)
Reproductive	0.775 \pm 0.028 (75)	0.818 \pm 0.023 (19)	0.800 \pm 0.033 (90)	0.766 \pm 0.035 (47)	0.799 \pm 0.040* (68)	0.621 \pm 0.082* (21)

DISCUSSION

Getz et al. (2006) concluded that beginning population density and length of the increase period were responsible for variation in amplitudes of population fluctuation of *M. ochrogaster*. Cessation of population growth, which determined length of the increase and thus “peak” densities, resulted from decreased survival. Variation in amplitude also was influenced by site-specific conditions, for example, cover and food (Getz et al. 2005b). In the present analysis, we addressed 2 additional aspects of population fluctuations: Why fluctuations occur some years and not others, and what demographic variables are responsible for the fluctuations.

Our results support hypotheses predicting that greater survival, but not increased reproduction, is responsible for generation of population fluctuations of *M. ochrogaster*. Although earlier age at 1st reproduction has been suggested to be an important demographic determinant of the initiation of a population fluctuation (Oli and Dobson 1999; Ozgul et al. 2004; Prévot-Julliard et al. 1998), our data did not allow a rigorous test of this hypothesis. Thus, we agree with Norrdahl and Korpimäki (2002b) on the role of survival in driving population fluctuations in arvicoline rodents.

Factors influencing the interval between population fluctuations are not well known (Boonstra et al. 1998). Evidence for reduced habitat quality due to high population density derives mainly from manipulative studies in which predators were excluded (Klemola et al. 2000) or emigration was prevented (Krebs et al. 1973), which in turn resulted in exceptionally high population densities (Agrell et al. 1995; Klemola et al. 2000). Norrdahl and Korpimäki (2002a) observed a 12-month lag in recovery of individual quality, longer than the life span of most animals in the population. They concluded that a lag in recovery of the quality of voles from effects of previous high densities represented indirect effects from changes in the biotic environment. Saucy (1984) concluded that delayed density-

dependent factors fit a predator–prey model rather than habitat degradation. Although we did not measure condition of the voles or changes in environmental quality over time, we found no correlation between peak density and the interval between population fluctuations that was consistent with presumed effects on condition of individuals or reduced habitat quality due to high peak density.

We presumed that variation in survival rates was a result of in situ mortality; emigration was not a major demographic factor in our populations (Getz et al. 2005a; Verner and Getz 1985). We further assumed predation to have been the primary source of mortality in our populations (Getz 2005; Getz et al. 2006). Our study area hosted 21 species of predators: 8 raptors, 5 large carnivores, 3 small carnivores, and 5 snakes (Lin and Batzli 1995). Of these predators, only 1 (least weasel [*Mustela nivalis*]) is a resident vole specialist, whereas the other vole specialist (rough-legged hawk [*Buteo lagopus*]) is a winter migrant present November through March. Thus, most of the predators present during the period of population growth were generalists. Demography in the individual study sites appeared to be site-specific; most fluctuations and the peak densities were asynchronous (Getz et al. 2001). Because of its small size, the study area undoubtedly constituted only a small portion of the foraging area of individual mammalian and avian, and perhaps snake (Keller and Heske 2000), predators. Predators feeding in our study sites would, therefore, also prey extensively upon other species in habitats outside the study area.

Desy and Batzli (1989) and Lin and Batzli (1995) concluded from studies conducted in experimental enclosures adjacent to our study sites that generalist predators could exhibit rapid numerical responses (by switching feeding sites) to locally high population densities of voles. Korpimäki and Norrdahl (1991) concluded that predation by generalist predators tends to dampen population fluctuations. However, the contribution of individual predator species to overall mortality of voles would

have varied from year to year because population densities of generalist predator species most likely were controlled by other factors in addition to vole densities within our study sites. Because of the independent nature of population fluctuations of such diverse predator species as raptors, large and small mammals, and snakes, as well as variation in numerical and functional responses of these predators (Pearson 1985), we speculate the net effects of predation may be greater in some years, suppressing population growth, than in others, allowing population growth to occur (Gilg et al. 2003; Norrdahl and Korpimäki 2002b; Pearson 1985).

Although the role of predation in population fluctuations of arvicoline rodents is controversial (e.g., Graham and Lambin 2002; Korpimäki and Norrdahl 1998; Oli 2003), our results suggest that predation played an important role in the dynamics of our study populations. If our speculations regarding variation in the amount of predation pressure are valid, timing of population fluctuations would be expected to be erratic, with no typical delayed density-dependent predator-prey cycle, and no consistent interval between population fluctuations. This is what we observed with respect to population fluctuations of *M. ochrogaster* over the 25 years of our study. We therefore suggest that, although amplitude of population fluctuation of voles was in part intrinsic and site specific, occurrence of fluctuations resulted from factors extrinsic to the study sites that controlled predator populations.

ACKNOWLEDGMENTS

The study was supported in part by National Science Foundation grant DEB 78-25864 and National Institutes of Health grant HD 09328 and by the University of Illinois School of Life Sciences and Graduate College Research Board. We thank the following individuals for their assistance with fieldwork: L. Verner, R. Cole, B. Klatt, R. Lindroth, D. Tazik, P. Mankin, T. Pizzuto, M. Snarski, S. Buck, K. Gubista, S. Vanthernout, M. Schmierbach, D. Avalos, L. Schiller, J. Edgington, B. Frase, and the 1,063 undergraduate "mouseketeers" without whose extra hands in the field the study would not have been possible. C. Haun, M. Thompson, and M. Snarski entered the data sets into the computer.

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Submitted 18 April 2005. Accepted 22 August 2005.

Associate Editor was Douglas A. Kelt.