

1 Running Head: Demography of vole populations

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3 Demography of fluctuating vole populations:

4 Are changes in demographic variables consistent across
5 individual cycles, habitats and species?

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22 Abstract. We analyzed monthly survival rates, persistence of
23 young, reproduction, recruitment of young, immigration rates,
24 body mass, and sex ratio for fluctuating sympatric populations

1 of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa,
2 bluegrass and tallgrass over 25 years. *M. ochrogaster* underwent
3 13 population cycles in alfalfa, 12 in bluegrass and five in
4 tallgrass. *M. pennsylvanicus* displayed five cycles in alfalfa,
5 nine in bluegrass and was acyclic in tallgrass. Among the
6 demographic variables considered, only increased survival and
7 persistence of young were associated consistently with the
8 increase phase of population cycles in both species. Survival
9 rates, persistence of young and reproduction of *M. ochrogaster*
10 were lower during the decline than during the increase phase in
11 alfalfa and bluegrass, but not in tallgrass. There were no
12 demographic differences between the decline and increase phases
13 for *M. pennsylvanicus* in either alfalfa or bluegrass. Most
14 differences in demographic variables within phases among
15 habitats involved survival and explained among-habitat
16 demographic differences of each species. Differences in
17 demographic variables within phases between species also mainly
18 involved survival; these differences were consistent with
19 differences in demography of the two species in alfalfa.
20 Overall, our data indicate that changes in survival were most
21 important in determining patterns of fluctuation in our study
22 populations.

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

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Introduction

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

11 Considerable variation has been observed in the
12 configuration of population fluctuations among species and among
13 populations of the same species (Bjørnstad et al. 1998, Krebs
14 and Myers 1974, Saitoh et al. 1998). Within a species,
15 populations occupying different habitats in the same region may
16 display erratic, annual or multi-annual fluctuations (Taitt and
17 Krebs 1985, Lidicker 1988). Populations of a species within the
18 same site may display annual fluctuations at some times and
19 multi-annual cycles at other times (Marcström et al. 1990).
20 Species with similar habitat requirements may display different
21 cyclic phenomena, and species with different requirements may
22 display similar cycles in the same site (Krebs et al. 1969,
23 Taitt and Krebs 1985, Getz et al. 1987, Marcström et al. 1990).
24 It is small wonder that simple explanations of population

1 fluctuations of arvicoline rodents have been elusive. In excess
2 of 22 hypotheses have been proposed to explain cyclic phenomena
3 in arvicoline rodents, but still no consensus has been reached
4 yet concerning the causes of population cycles (Batzli 1992,
5 1996, Oli and Dobson 1999, 2001).

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

23 We also need to test for differences in demographic
24 variables: (1) within phases among cycles within a habitat, (2)

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

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

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

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Methods

Species

Microtus ochrogaster

14 *M. ochrogaster* is characteristic of graminoid habitats and
15 monocots are a component of its diet; however, forbs are
16 required for maximum population success (Zimmerman 1965, Meserve
17 1971, Cole and Batzli 1978, 1979, Haken and Batzli 1996).

18 Although *M. ochrogaster* populations achieve high population
19 densities in habitats with dense cover (Birney et al. 1976),
20 this species is successful in habitats with relatively sparse
21 vegetative cover (Klatt 1986, Klatt and Getz 1987, Getz and
22 Hofmann 1999, Lin and Batzli 2001). High kidney efficiency of
23 *M. ochrogaster* results in relatively low water requirements
24 (Getz 1963), allowing the species to occupy dry grasslands.

Microtus pennsylvanicus

1 Although *M. pennsylvanicus* prefers succulent forbs
2 (Thompson 1965, Lindroth and Batzli 1984), it is successful when
3 feeding on a diet consisting mainly of graminoids (Cole and
4 Batzli 1978, 1979, Haken and Batzli 1996). *M. pennsylvanicus*,
5 therefore, may be abundant in primarily graminoid habitats (Getz
6 and Hofmann 1999). *M. pennsylvanicus* is most abundant in
7 habitats providing dense vegetative cover throughout the year
8 (Getz 1970, Birney et al. 1976, Klatt 1986, Klatt and Getz 1987,
9 Lin and Batzli 2001). Because of low kidney efficiency (Getz
10 1963), the species is characteristic of moist situations (Miller
11 1969). *M. pennsylvanicus* did not occur in the study region
12 prior to 1972 (Getz et al. 1978); the species first appeared in
13 the study sites in May 1973.

14

15 Study sites

16 The study sites were located in the University of Illinois
17 Biological Research Area ("Phillips Tract") and Trelease
18 Prairie, both 6 km NE of Urbana, Illinois (40°15'N, 88°28'W).
19 We monitored populations of *M. ochrogaster* and *M. pennsylvanicus*
20 in three habitats: restored tallgrass prairie (March 1972--May
21 1997), bluegrass, *Poa pratensis*, (January 1972--May 1997) and
22 alfalfa, *Medicago sativa*, (May 1972--May 1997). Tallgrass
23 prairie was the original habitat of both species in Illinois,
24 while bluegrass, an introduced species, represents one of the

1 more common habitats in which the two species can be found today
2 in Illinois. Alfalfa is an atypical habitat that provides
3 exceptionally high-quality food for both species (Cole and
4 Batzli 1979, Lindroth and Batzli 1984). We have described the
5 study sites in detail elsewhere (Getz et al. 1979, 1987, 2001)
6 and thus provide only brief descriptions here.

7 We trapped sites in two restored tallgrass prairies: one
8 located in Trelease Prairie and the other in Phillips Tract.
9 Relative abundance of the predominant plant species in Trelease
10 Prairie were as follows: big bluestem, *Andropogon gerardii*
11 (17%); bush clover, *Lespedeza cuneata* (16%); ironweed, *Vernonia*
12 (12%); Indian grass, *Sorghastrum nutans* (10%); about 15 other
13 species with relative abundances of <10% (Getz et al. 1979).
14 Lindroth and Batzli (1984) recorded relative abundances of the
15 most prominent plant species in the Phillips site: *A. gerardii*
16 (38%); *L. cuneata* (25%); Beard tongue foxglove, *Penstemon*
17 *digitalis* (16%); and *S. nutans* (19%). All other species
18 represented < 1% relative abundance. Both prairies were burned
19 during the spring at 3-4-year intervals to control invading
20 shrubs and trees. We trapped sites in one or both of the
21 tallgrass prairies, depending upon requirements of the overall
22 study at the time. Vole populations fluctuated in synchrony in
23 the two tallgrass areas (Getz and Hofmann 1999).

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

10 Two alfalfa sites in Phillips Tract were trapped during the
11 study. A site was trapped until invading forbs and grasses
12 began to crowd out the alfalfa. One year before trapping was
13 terminated in that site, the other was planted with alfalfa so
14 that the alfalfa would be fully developed when trapping
15 subsequently commenced in that site. Sites were separated by a
16 10-m closely mown strip. Animals moved between the two sites,
17 however, so we presumed we were monitoring a single population

18 Initially, *M. sativa* comprised 75% of the vegetation in
19 each site. During the last year of usage, other common plants
20 included: *P. pratensis*; goldenrod, *Solidago*; timothy, *Phleum*
21 *pratense*; brome grass, *Bromus inermis*; clover, *Trifolium repens*
22 and *T. pratense*; and plantain, *Plantago*. A series of 3-m wide
23 strips were mowed 25 cm above the surface periodically each
24 June-September to control invading weedy forbs and to promote

1 new growth of alfalfa. Mowing of the strips was timed so that
2 at least two-thirds of the field had dense vegetative cover at
3 all times.

4

5 Habitat quality

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

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

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

22

23 Procedures

1 All study sites were organized on a grid system with 10-m
2 intervals. One wooden multiple-capture live-trap (Burt 1940)
3 was placed at a station. Each month a 2-day prebaiting period
4 was followed by a 3-day trapping session. Cracked corn was used
5 for prebaiting and as bait in traps. We used vegetation or
6 aluminum shields to protect traps from the sun during summer.
7 Wooden traps provided ample insulation in winter, and thus we
8 did not provide nesting material in the traps at any time. We
9 estimated trap mortality to be <0.5%.

10 Traps were set in the afternoon and checked at about 0800 h
11 and 1500 h on the following 3 days. All animals were toe-
12 clipped (≤ 2 toes on each foot) at 1st capture for individual
13 identification. Although toe clipping no longer is a
14 recommended method of marking animals, during most of the time
15 of the study, few alternative methods were available. Ear tags
16 were available, but owing to frequent loss of tags, toe clipping
17 was deemed a more effective means of marking individuals. The
18 field protocol, including use of toe clipping, was reviewed
19 periodically by the University of Illinois Laboratory Animal
20 Resource Committee throughout the study. The committee approved
21 the field protocol, based on University and Federal guidelines,
22 as well as those recommended by the American Society of
23 Mammalogists, in effect at the time.

1 Species, individual identification, grid station, sex,
2 reproductive condition (males: testes abdominal or descended;
3 females: vulva open or closed, pregnant as determined by
4 palpation, or lactating), and body mass to the nearest 1 g were
5 recorded at each capture.

6

7 Data analysis

8 We estimated the density of voles for each trapping session
9 using the minimum number alive method (MNA, Krebs 1966, 1999).
10 Previously marked individuals not captured in a given trapping
11 session, but trapped in a subsequent session, were considered to
12 have been present during sessions in which they were not
13 captured. Although the Jolly-Seber index is recommended for
14 estimating population density (Efford 1992), at least 10
15 individuals must be trapped each session in order to obtain
16 reasonable estimates (Pollock, et al. 1990). During months
17 voles were present in the study sites, 10 or fewer *M.*
18 *ochrogaster* were trapped 26%, 52% and 62% percent of trapping
19 sessions in alfalfa, bluegrass, and tallgrass, respectively.
20 Ten or fewer *M. pennsylvanicus* were trapped 55% of the sessions
21 in alfalfa, 46% in bluegrass, and 24% in tallgrass. Since the
22 same index should be used throughout, we felt justified in using
23 MNA. Further, since we utilized prebaited multiple-capture
24 live-traps checked twice daily for 3 days each session, our

1 capture efficiency was very high. Of the animals estimated to
2 be present, 92% of the *M. ochrogaster* and 91% of the *M.*
3 *pennsylvanicus* were actually captured each session.

4 A population cycle was presumed to have occurred when
5 population fluctuations exceeded the following densities: *M.*
6 *ochrogaster*–alfalfa, 75/ha; bluegrass, 35/ha; tallgrass, 30/ha;
7 *M. pennsylvanicus*–alfalfa and bluegrass, 25/ha (*M.*
8 *pennsylvanicus* was acyclic in tallgrass; Getz et al. 2001).
9 Each cycle included trough, increase, peak, and decline phases.
10 As described below, the peak period of most population cycles of
11 both species was only one month in duration. In effect, most of
12 our study populations increased to a peak density one month and
13 then declined rapidly the following month (Figs. 1 and 2).
14 Thus, “peaks” represent only a high point in the fluctuations
15 rather than a true “phase”. Nevertheless, we have included the
16 peak period as a separate phase in our analyses to provide a
17 comparison with results of other studies. Beginning and
18 termination of each phase for each cycle was based on major
19 inflections in population change for that phase and cycle.

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

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Demographic variables

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

1 month, as was the proportion of new animals (those first caught
2 a given month) that were immigrants.

3

4 Body mass

5 Body mass is an indirect indicator of quality of the
6 animals, in that individuals in good condition would be expected
7 to have higher body mass than those in poor condition. We
8 limited our examination of body mass to adult males (≥ 30 g). In
9 this way, we avoided bias from variation in the proportion of
10 the population comprised of young animals and from variation in
11 the reproductive status of females (i.e., changes in body mass
12 due to pregnancy and parturition). We recognize that during the
13 winter, body mass of some adult males dropped below 30 g,
14 perhaps resulting in a slight, but not critical, bias during
15 this period.

16

17 Sex ratio

18 We compared sex ratio of the adult population among phases
19 to determine any possible relationship with population cycling.
20 The proportion of the adult (≥ 30 g) population composed of males
21 was utilized in the analysis of sex ratios among phases of
22 population cycles.

23

1 Statistical analyses

2 Because most of the variables did not meet the requirements
3 for normality (population densities and demographic variables
4 were non normal at the 0.05 level; Kolmogorov-Smirnov test, Zar
5 1999), we log-transformed all variables. Variables that
6 included "zeros" were log (X+1)-transformed because logarithm of
7 zero is not defined. We used 2-sample t-tests, and one-way
8 ANOVAs followed by Tukey's honestly significant difference (HSD)
9 post-hoc multiple comparison tests. Degrees of freedom (df) for
10 "persistence of young" are actual numbers of individuals
11 involved; all other df values represent the number of months of
12 data. When degrees of freedom for t-tests are given in whole
13 numbers, variances are equal (Levene's test for equality of
14 variances); when variances were not equal, df is given to one
15 decimal place. All statistical analyses were performed using
16 SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001).

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Results

19 Population densities

20 *Microtus ochrogaster*

21 Mean population density over the 25 years of the study in
22 alfalfa (50/ha) was higher than that in bluegrass (18/ha) which,
23 in turn, was higher than that in tallgrass (7/ha; Getz et al.
24 2001). There were 13 population cycles in alfalfa (Fig. 1),

1 with a mean peak density of 202/ha (range, 77-638/ha), 12 in
2 bluegrass with a mean peak density of 67/ha (range, 25-156/ha)
3 and five in tallgrass with a mean peak density of 59/ha (range,
4 34-92/ha). Peak densities differed among habitats ($F = 11.7846$,
5 $df = 2,26$, $P = 0.0002$), with mean peak density in alfalfa being
6 significantly higher than those in bluegrass and tallgrass ($P <$
7 0.05). There was no difference between mean peak densities in
8 bluegrass and tallgrass ($P > 0.05$). Amplitudes of fluctuations
9 also differed among habitats ($F = 9.486$, $df = 2,25$, $P = 0.001$),
10 with significantly higher amplitudes in alfalfa (175/ha) than in
11 bluegrass and tallgrass (57 and 53/ha, respectively; $P < 0.05$).
12 Amplitudes of fluctuation did not differ in bluegrass and
13 tallgrass ($P > 0.05$).

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

19 *Microtus pennsylvanicus*

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

1 *Microtus pennsylvanicus* was acyclic in tallgrass, with a
2 maximum density of 128/ha (Fig. 2; Getz et al. 2001). There
3 were five population fluctuations in alfalfa with a mean peak
4 density of 53/ha (range, 29-79/ha) and nine fluctuations in
5 bluegrass, with a mean peak density of 56/ha (range, 35-91/ha).
6 Peak densities ($t = 0.45$, $df = 12$, $P = 0.658$) and amplitudes of
7 fluctuation in alfalfa and bluegrass did not differ (47/ha and
8 44/ha, respectively; $t = 0.135$, $df = 12$; $P = 0.895$). *M.*
9 *pennsylvanicus* was either absent or in very low population
10 densities for longer periods in alfalfa than in bluegrass (Fig
11 2).

12

13 Demographic variables

14 *Microtus ochrogaster*

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

1 trough, and survival of young was greater during the increase
2 than during the trough.

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

7 The proportions of reproductive adult males and females
8 were significantly lower during the decline than during the
9 increase phase in alfalfa (Table 1) and all other phases in
10 bluegrass (Table 2). There was no difference in the proportion
11 of either sex reproductive during the peak and decline in
12 alfalfa (Table 1). The only difference in proportion of
13 reproductive adults between the trough and increase in all three
14 habitats was a greater proportion of reproductive males during
15 the increase in alfalfa (Table 1). Fewer females were
16 reproductive during the decline than during the trough in
17 alfalfa (Table 1) and tallgrass (Table 3), as were both sexes in
18 bluegrass (Table 2). There was no difference in the proportion
19 of males reproductive among the four phases in tallgrass (Table
20 3).

21 We found no difference regarding the proportions of the
22 population comprised of young born into the population in either
23 alfalfa (Table 1) or bluegrass (Table 2). However, the
24 proportion of the population comprised of young was greater

1 during the trough than during the increase in tallgrass (Table
2 3). Also, in tallgrass, immigrants made up a significantly
3 smaller proportion of the total population, as well as of the
4 new animals, during the decline than during the increase (Table
5 3).

6

7 *Microtus pennsylvanicus*

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

21 The proportions of males and females that were reproductive
22 were lowest during the decline in alfalfa (Table 4). Although a
23 similar pattern emerged in bluegrass, the differences were not
24 significant (Table 6). Proportions of the population comprised

1 of young animals did not differ among the four phases in alfalfa
2 (Table 4); the proportion of the population comprised of young
3 animals was less during the trough than during the decline in
4 bluegrass (Table 5). Proportions of immigrants did not differ
5 among phases in either alfalfa (Table 4) or bluegrass (Table 5).
6 However, the proportions of new animals that were immigrants
7 were greater during the trough and peak than during the increase
8 and decline in bluegrass (Table 5).

9

10 Comparison of demographic variables among phases

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

20

21 Within phases among cycles within each habitat

22 With the exception of the trough, individual phases of each
23 population cycle were only a few months in duration. As a
24 result, there were few data regarding several demographic

1 variables for most cycles. Sufficient data were available for
2 analysis of total population survival and proportion of females
3 reproductive for the trough, increase and decline phases of most
4 cycles within each habitat. Comparisons of peak phases were not
5 possible because peaks typically were only one month in
6 duration.

7 *Microtus ochrogaster*.--Total survival during the 1991-1993
8 trough (Fig. 1) in alfalfa was lower than that of the other
9 cycles ($F = 3.400$, $df = 7,130$, $P = 0.002$). When this cycle was
10 removed from the analysis, there was no difference among the
11 other cycles ($F = 1.897$, $df = 6,121$, $P = 0.087$). During the
12 decline of 1975-1976, total population survival was
13 exceptionally high. There was no difference in survival among
14 the declines of the remaining cycles ($F = 1.375$, $df = 11,37$, $P =$
15 0.225). A significant difference ($F = 2.183$, $df = 11,37$, $P =$
16 0.038) in proportion of females reproductive among the decline
17 phases in alfalfa resulted from a higher proportion of
18 reproductive females during the 1987 decline; when this cycle
19 was removed from analysis, the difference disappeared ($F =$
20 1.954 , $df = 10,32$, $P = 0.074$).

21 Survival during four of the increase phases varied
22 significantly among the cycles in bluegrass (two unusually high,
23 1982, 1987; two unusually low, 1991, 1993; $F = 5.161$, $df =$
24 $11,35$, $P < 0.001$). Only one specific cycle, each, in the trough

1 (1991-1993) and decline (1982) was responsible for the
2 significant differences with respect to proportion of the
3 females reproductive among these phases in bluegrass ($F = 2.615$,
4 $df = 11,79$, $P = 0.007$ and $F = 2.811$, $df = 10,35$, $P = 0.011$,
5 respectively). When these cycles were removed from the
6 analyses, the proportion of reproductive females did not differ
7 among phases of the remaining cycles (trough: $F = 1.866$, $df =$
8 $10,66$, $P = 0.066$; decline: $F = 1.091$, $df = 9,32$, $P = 0.396$).

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

11 *Microtus pennsylvanicus*.--There were only two significant
12 demographic differences within each phase among the various
13 population cycles in alfalfa and bluegrass, both involving
14 proportion of females that were reproductive. In alfalfa, the
15 only difference in the proportion of females reproductive during
16 the decline was between the declines of 1980-1981 and 1995-1996
17 ($F = 4.894$, $df = 3,17$, $P = 0.012$). In bluegrass, a significant
18 difference among cycles in the proportion of females
19 reproductive during the increase ($F = 3.081$, $df = 8,34$, $P =$
20 0.010) was attributed to very low reproduction during the 1985-
21 1986 cycle. When this cycle was removed from the analysis, the
22 difference disappeared ($F = 2.201$, $df = 7,30$, $P = 0.063$). Total
23 population survival during the trough, increase and decline
24 phases did not differ among the cycles in either habitat.

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Phases within cycles among habitats

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

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

1 5.802, $df = 2,660$, $P = 0.003$); (6) greater proportion of
2 reproductive males during the increase in alfalfa than in either
3 bluegrass or tallgrass ($F = 4.627$, $df = 2,133$, $P = 0.016$); (7)
4 lesser proportion of reproductive females during the increase in
5 tallgrass than in either alfalfa or bluegrass ($F = 6.297$, $df =$
6 $2,135$, $P = 0.002$).

7 The remaining differences in the demographic variables, all
8 involving reproduction or immigration, were not consistent with
9 among-habitat differences in population densities: (1) greater
10 proportion of young during the trough in tallgrass than in
11 either alfalfa or bluegrass ($F = 18.505$, $df = 2,365$, $P < 0.001$;
12 (2) lesser proportion of new animals consisting of immigrants
13 during the trough in tallgrass than in either bluegrass or
14 alfalfa ($F = 10.929$, $df = 2,240$, $P = 0.001$); (3) greater
15 percentage of new animals that were immigrants during the
16 increase in tallgrass than in bluegrass ($F = 3.808$, $df = 2,71$, P
17 $= 0.027$) (4) greater proportion of young during the decline in
18 tallgrass than in alfalfa ($F = 3.668$, $df = 2,117$, $P = 0.028$);
19 (5) lesser proportion of reproductive males during the decline
20 in bluegrass than in either alfalfa or tallgrass ($F = 4.089$, df
21 $= 2,111$, $P = 0.019$).

22 *Microtus pennsylvanicus*.--Four significant differences in
23 demographic variables, involving survival and persistence of
24 young within given phases of the two habitats, all resulted from

1 higher values in bluegrass than in alfalfa and were consistent
2 with higher population densities in bluegrass as compared to
3 alfalfa: (1) greater total population survival during the
4 decline: $t = 2.20$, $df = 53$, $P = 0.032$; (2) greater adult
5 survival during the decline: $t = 2.17$, $df = 43$, $P = 0.036$; (3)
6 longer persistence of young during the increase: $t = 2.26$, $df =$
7 131.1 , $P = 0.009$; (4) longer persistence of young during the
8 peak: $t = 2.73$, $df = 48.4$, $P = 0.009$. Three instances of
9 differences in proportions of reproductive adults, none of which
10 agreed with higher population densities in bluegrass than in
11 alfalfa, were: (1) greater proportion of reproductive females
12 during the trough in alfalfa ($t = 2.93$, $df = 116$, $P = 0.004$; (2)
13 greater proportion of reproductive males during the trough in
14 alfalfa; $t = 2.015$, $df = 125.9$, $P = 0.046$; and (3) greater
15 proportion of reproductive males during the increase in alfalfa;
16 $t = 3.113$, $df = 44.0$, $P = 0.003$. Two of the remaining four
17 significant differences involved greater proportions of
18 immigrants in alfalfa during the increase ($t = 2.57$, $df = 53$, P
19 $= 0.013$) and a greater proportion of immigrants during the
20 decline in bluegrass than in alfalfa ($t = 2.52$, $df = 34.6$, $P =$
21 0.017); only the latter difference was consistent with
22 differences in population densities between the two habitats.
23 The remaining two demographic differences involved greater
24 proportion of young in alfalfa during the trough ($t = 2.76$, $df =$

1 129.5, $P = 0.011$) and increase ($t = 2.53$, $df = 59.7$, $P = 0.014$);
2 these differences were inconsistent with higher densities in
3 bluegrass.

4

5 Interspecific comparisons among phases

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

11 Alfalfa.--Most differences between the two species in
12 alfalfa involved the increase and peak phases. Five differences
13 involved greater survival of *M. ochrogaster* than *M.*
14 *pennsylvanicus* and reflected higher population densities of the
15 former species in alfalfa: (1) total population survival during
16 the trough ($t = 3.55$, $df = 151.4$, $P = 0.001$), (2) total
17 population survival during the increase ($t = 4.067$, $df = 83$, $P <$
18 0.001); (3) adult survival during the increase ($t = 2.026$, $df =$
19 82 , $P = 0.046$); (4) adult survival during the peak ($t = 2.20$, df
20 $= 16.8$, $P = 0.042$; and (5) young survival during the peak ($t =$
21 3.32 , $df = 21$, $P = 0.003$). Only two differences involved
22 reproduction: young comprised a greater proportion of the
23 population of *M. ochrogaster* than *M. pennsylvanicus* during the
24 increase ($t = 3.167$, $df = 86$, $P = 0.002$) and peak phases ($t =$

1 4.019, $df = 27$, $P = 0.001$). These, too, were consistent with
2 differences in densities of the two species in alfalfa.

3 Other comparisons of the increase and peak phases were not
4 consistent with differences in population densities of the two
5 species in alfalfa. The proportion of reproductive male *M.*
6 *pennsylvanicus* was greater than that of *M. ochrogaster* during
7 the trough ($t = 2.709$, $df = 166.1$, $P = 0.007$) and increase ($t =$
8 2.783 , $df = 85$, $P = 0.007$), while there was no difference in the
9 proportion of females reproductive between the two species
10 during these phases. Proportion of immigrants in the population
11 generally was greater for *M. pennsylvanicus* than *M. ochrogaster*
12 during the increase (proportion of the population and of new
13 animals; $t = 2.549$, $df = 37$, $P = 0.015$ and $t = 2.455$, $df = 37$, P
14 $= 0.019$) and the proportion of new animals that were immigrant
15 was greater during the peaks ($t = 3.362$, $df = 14$, $P = 0.005$).
16 Demographic variables did not differ between the two species
17 during the decline phase.

18 Bluegrass.--There were few differences between *M.*
19 *ochrogaster* and *M. pennsylvanicus* with respect to most
20 demographic variables during all four phases of the population
21 cycle in bluegrass. Survival of adult *M. pennsylvanicus* was
22 greater than that of *M. ochrogaster* during the trough ($t =$
23 2.887 , $df = 138.1$, $P = 0.005$), and total population survival of
24 *M. pennsylvanicus* was also greater during the decline ($t =$

1 3.119, $df = 68$, $P = 0.003$). The proportion of young animals
2 during the trough ($t = 2.824$, $df = 242.9$, $P = 0.005$) and the
3 proportion of new animals that were immigrants during the
4 decline ($t = 2.55$, $df = 52$, $P = 0.014$) were greater for *M.*
5 *ochrogaster* than for *M. pennsylvanicus*. The proportion of *M.*
6 *ochrogaster* females reproductive was greater than that of *M.*
7 *pennsylvanicus* during the trough ($t = 2.985$, $df = 122.8$, $P =$
8 0.003) and increase phases ($t = 3.77$, $df = 76$, $P < 0.001$).

9

10 Seasonal effects on demographic variables

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

23 *Microtus ochrogaster* population cycles typically peaked
24 during autumn or winter in both alfalfa and bluegrass, while

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

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

13

14 *Microtus ochrogaster*

15 In alfalfa, total population monthly survival during
16 summers of cycle years was greater than that for non-cycle years
17 (0.606 ± 0.030 and 0.433 ± 0.056 , respectively; $t = 2.899$, $df =$
18 43.1 , $P = 0.006$). Survival during autumn of cycle years was
19 also greater than during non-cycle years (0.654 ± 0.021 and
20 0.426 ± 0.057 , respectively; $t = 3.9$, $df = 31.5$, $P < 0.001$).
21 Survival during the winter of population declines did not differ
22 from that during years without winter declines (0.504 ± 0.039
23 and 0.515 ± 0.056 , respectively; $t = 0.037$, $df = 67$, $P = 0.971$).

1 In bluegrass, there also was greater survival during the
2 summer and autumn of cycle years as compared to non-cycle years
3 (Summer: 0.487 ± 0.048 and 0.307 ± 0.063 , respectively; $t =$
4 2.559 , $df = 54.1$, $P = 0.013$. Autumn: 0.566 ± 0.026 and $0.401 \pm$
5 0.058 , respectively; $t = 2.987$, $df = 39.9$, $P = 0.005$). As in
6 alfalfa, there was no difference in survival in bluegrass during
7 winters with a population decline and winters without a decline
8 (0.503 ± 0.044 and 0.420 ± 0.058 , respectively; $t = 1.449$, $df =$
9 58.2 , $P = 0.153$).

10 In alfalfa, there was no difference in the proportion of
11 females reproductive in summers when the population was
12 increasing in numbers as contrasted to summers without an
13 increase phase (0.913 ± 0.21 and 0.901 ± 0.038 , respectively; t
14 $= 0.358$, $df = 56$, $P = 0.722$). Similarly, there was no
15 difference in the proportion of females reproductive in autumns
16 with population increases as compared to autumns without
17 increases (0.867 ± 0.019 and 0.815 ± 0.054 , respectively; $t =$
18 1.106 , $df = 30.3$, $P = 0.277$). Finally, there was no difference
19 in the proportion of females reproductive during winters with
20 population declines and winters without declines (0.378 ± 0.044
21 and 0.436 ± 0.061 , respectively; $t = 0.756$, $df = 56$, $P = 0.453$).

22 Similar results for the increase phase were observed
23 regarding the bluegrass populations. Proportion of females
24 reproductive during summer (0.825 ± 0.044 and 0.887 ± 0.056 ,

1 respectively; $t = 0.665$, $df = 41$, $P = 0.510$) or autumn ($0.842 \pm$
2 0.024 and 0.905 ± 0.043 , respectively; $t = 0.830$, $df = 54$, $P =$
3 0.410) did not differ between cycle and non cycle years. During
4 the winter, more females were reproductive when there was no
5 population decline than when the population was in a decline
6 phase (0.672 ± 0.077 and 0.328 ± 0.058 , respectively; $t = 3.327$,
7 $df = 47$, $P = 0.002$).

8

9 *Microtus pennsylvanicus*

10 Survival of the total population of *M. pennsylvanicus* was
11 greater during the spring of cycle than for non-cycle years
12 (0.678 ± 0.038 and 0.464 ± 0.047 , respectively; $t = 3.810$, $df =$
13 68.2 , $P < 0.001$), summer (0.590 ± 0.029 and 0.436 ± 0.044 ; $t =$
14 3.44 , $df = 76.4$, $P = 0.001$) and autumn (0.552 ± 0.042 and 0.407
15 ± 0.042 ; $t = 2.597$, $df = 71.1$, $P = 0.011$).

16 There was no difference in the proportion of females
17 reproductive during the spring of cycle and non-cycle years
18 (0.686 ± 0.048 and 0.688 ± 0.062 , respectively; $t = 0.249$, $df =$
19 55.5 , $P = 0.805$), summer (0.683 ± 0.042 and 0.770 ± 0.060 ; $t =$
20 0.788 , $df = 50.6$, $P = 0.434$) and autumn (0.760 ± 0.039 and 0.827
21 ± 0.039 ; $t = 0.680$, $df = 77$, $P = 0.498$).

22

23 Body mass

1 For *Microtus ochrogaster*, adult male body mass was higher
2 during the increase and peak than during the trough and decline
3 in alfalfa and bluegrass (Table 6). When body mass differences
4 between increase/peak and decline/trough were compared for only
5 those cycles that peaked during spring/summer (alfalfa, 1;
6 bluegrass, 3) the difference approached significance
7 (increase/peak, $40.1 \pm 0.3\text{g}$; decline/trough, $39.2 \pm 0.3\text{g}$; $t =$
8 1.764 , $df = 578.9$, $P = 0.078$). There was no difference between
9 the increase/peak and decline/trough in tallgrass. However,
10 adult male body mass during the decline was higher than during
11 the trough than the peak in tallgrass (Table 6). For *M.*
12 *pennsylvanicus*, adult male body mass did not vary significantly
13 among the four phases of the population cycle in either alfalfa
14 or bluegrass (Table 6).

15 Body mass of adult males is significantly lower during the
16 winter than during other seasons (Getz et al. In Review a).
17 Since most population cycles of *M. ochrogaster* declined during
18 winter, we compared differences in body mass during the winter
19 of cycle and non cycle years. Differences were significantly
20 lower during cycle years (Alfalfa: $F = 13.193$, $df = 3, 2889$, $P <$
21 0.001 . Bluegrass: $F = 14.187$, $df = 3, 1263$, $P < 0.001$), but not
22 during non cycle years (Alfalfa: $F = 0.682$, $df = 3, 878$, $P =$
23 0.563 . Bluegrass: $F = 2.333$, $df = 3, 171$, $P = 0.076$).

24

1 Sex ratio

2 There was no difference in sex ratios among the four phases
3 of the population cycles of either species in any habitat (Table
4 7).

5

6

Discussion

7 Changes in numbers associated with generation of a
8 population cycle are the net result of population losses from
9 mortality and emigration, and additions from reproduction and
10 immigration. Demographic variables are involved in four aspects
11 of population cycles: (1) initiation of population growth, (2)
12 continued growth to a high amplitude peak, (3) stoppage of
13 population growth at the peak, and (4) decline to low numbers.
14 For large-scale fluctuations in abundance to occur, one or more
15 demographic variables must change (Oli and Dobson 1999, 2001).
16 There is no lack of evidence for the involvement of demographic
17 variables in generating population cycles (Hoffman 1958, Krebs
18 et al. 1969, Keller and Krebs 1970, Krebs et al. 1973, Krebs and
19 Myers 1974, Gaines and Rose 1976, Boonstra 1977, Getz et al.
20 1979, Verner and Getz 1985, Batzli 1992, 1996, Krebs 1996, Oli
21 and Dobson 1999, Getz et al. 2000). However, there is no
22 consensus about which variables are most important among
23 temporally and spatially different population cycles of even one
24 species, let alone across species. The present study involved

1 analysis of demographic variables obtained during a 25-year
2 study of demography of *Microtus ochrogaster* and *M.*
3 *pennsylvanicus* in three habitats in east-central Illinois.

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

21 The change from an increase to a decline phase defines a
22 population cycle. The peak is merely a pivotal point at which
23 the population stops growing, followed by a decline in numbers
24 to form fluctuations of varying amplitudes. Thus, comparisons

1 of the increase and decline phases are important in
2 understanding the role of changing demographic variables in the
3 switch from population growth to population decline, which is
4 necessary to generate population cycles.

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

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

19 The only consistent seasonal effect on demographic
20 variables was a lower proportion of reproductive females of both
21 species during the winter in all three habitats. Because the
22 decline phase of most (22 of 30) cycles of *M. ochrogaster*
23 occurred during the winter (Getz et al. In Review c), density-
24 independent seasonal reduction in reproduction may have

1 contributed to winter population declines, but not to declines
2 in populations peaking in spring-summer (Getz et al. In Review
3 a). Although reproduction in *M. pennsylvanicus* declined during
4 the winter, most (10 of 14) declines began prior to winter.
5 Thus, seasonal influence on reproduction was not a primary
6 factor in generating most declines in this species.

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

14 There was considerable variation in demographic variables
15 associated with given phases among the three habitats. For both
16 species, most differences involved survival and persistence of
17 young and were consistent with demographic differences among the
18 habitats. Five of the seven differences among phases of *M.*
19 *ochrogaster* that explained demographic differences between
20 alfalfa and bluegrass involved survival; only two involved
21 reproduction. Three of the four differences that were
22 inconsistent with demography in the two habitats involved
23 reproduction. Similarly, for *M. pennsylvanicus*, all four
24 differences in survival within phases between alfalfa and

1 bluegrass populations were consistent with demographic
2 differences between the two habitats. Only two of the five
3 differences in reproductive variables explained demographic
4 differences between the two habitats. None of the other
5 differences was consistent with demographic differences between
6 alfalfa and bluegrass.

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

17 Adult male body mass of *M. ochrogaster* was significantly
18 greater during the increase/peak than during the decline/trough
19 in alfalfa and bluegrass populations peaking in autumn-winter.
20 Further, a winter decline in body mass was observed only during
21 years in which a population decline occurred during winter.
22 Lesser body mass during the decline/trough than during the
23 increase/peak of those populations peaking in spring/summer
24 approached significance. Taken together, these results suggest

1 that variation in individual quality, at least for males, may be
2 involved in population cycling in *M. ochrogaster*. However, we
3 conclude elsewhere that decreased quality of animals is not a
4 primary factor responsible for population declines (Getz et al.
5 In Review c). There was no indication of a relationship between
6 population density and quality of animals of *M. pennsylvanicus*.
7 There were no phase-specific differences in adult male body mass
8 in either alfalfa or bluegrass for this species.

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

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

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

3 Elsewhere we suggest that improvement in survival due to
4 relaxation of predation pressure is responsible for population
5 growth and high amplitude fluctuations in *M. ochrogaster* and *M.*
6 *pennsylvanicus* in our study sites (Getz et al. In Review b).
7 Density-dependent mortality caused by a resident specialist
8 predator (least weasel, *Mustela nivalis*), a seasonal specialist
9 predator (feral cat, *Felis silvestris*) and a migratory
10 specialist raptor (rough-legged hawk, *Buteo lagopus*), as well as
11 a number of generalist predators appears to be responsible for
12 cessation of population growth. Density-dependent intrinsic
13 factors affecting mortality may also play a role in stoppage of
14 population growth (Getz et al. In Review c). Predation pressure
15 from an array of resident generalist predators appears to be the
16 most likely reason for periods of low densities (Boonstra et al.
17 1998, Getz et al. In Review b).

18 While results of the present analyses are consistent with
19 these presumptions, we acknowledge that our results do not allow
20 conclusive rejection of alternative explanations (Boonstra 1994,
21 Oli and Dobson 1999, 2001). For example, phase-related changes
22 in age at first reproduction have been suggested to be an
23 important demographic determinant of the dynamics of cyclic
24 populations of small mammals (Oli and Dobson 1999, 2001), but

1 our data did not permit a rigorous test of this idea.
2 Nevertheless, our data do allow us to conclude that, among the
3 many demographic variables we considered, changes in survival
4 rates, presumably a consequence of variation in predation
5 pressure, contribute substantially to the numerical dynamics of
6 our study populations. We speculate that density-dependent
7 predation stops growth and triggers the decline phase. When
8 peak densities occur in autumn-winter (most populations of *M.*
9 *ochrogaster* and some of *M. pennsylvanicus* in alfalfa and
10 bluegrass), density-independent winter reduction in reproduction
11 may contribute to the initiation of the decline phase. For *M.*
12 *ochrogaster* and *M. pennsylvanicus* populations peaking in spring-
13 summer, decreased survival, presumably a result of predation by
14 generalist predators, appears to trigger the decline in
15 densities.

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Acknowledgements

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4

5

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

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

Table 1 (Cont.)

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

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

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

Table 2 (cont.)

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

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

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

Table 3 (Cont.)

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

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

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

Table 4 (Cont.)

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

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

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

Table 5 (Cont.)

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

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

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

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

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

Figure legends

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

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



