# Dynamics of sympatric vole populations: influence of food resources and interspecific competition

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Running head: Food resources and vole populations

## Summary

**1.** Abundance of food resources and interspecific competition can significantly influence the dynamics of arvicoline rodent populations.

**2.** We studied responses of *Microtus ochrogaster* and *M. pennsylvanicus* to supplemental food and interspecific competition in bluegrass (marginal food habitat) and tallgrass prairie (low food habitat). Removal experiments were conducted to study reciprocal interspecific interactions between the two species in bluegrass and the effects of *M. pennsylvanicus* on *M. ochrogaster* in tallgrass.

**3.** Mean population densities and patterns of fluctuation of *M. ochrogaster* did not differ between supplementally fed and control sites in either bluegrass or tallgrass habitats. However, amplitudes of fluctuation and proportion of reproductive females were higher in supplementally fed than in control bluegrass sites for this species. Mean population densities of *M. pennsylvanicus* were slightly higher in supplementally fed than in control tallgrass sites; the addition of food to bluegrass, however, did not result in higher population densities for this species.

**4.** Population densities of *M. ochrogaster* and M. *pennsylvanicus* in bluegrass were not suppressed by the presence of the other species. Although survival of *M. ochrogaster* was lower in the presence of *M. pennsylvanicus*, there was no negative effect on reproduction. Presence of *M. ochrogaster* did not adversely affect either survival or reproduction of *M. pennsylvanicus* in bluegrass. Although *M. pennsylvanicus* appeared to exert a strong suppressing effect on population densities of *M. ochrogaster* in tallgrass, neither survival nor reproduction of *M. ochrogaster* was lower when *M. pennsylvanicus* was present in this habitat. Similar results were observed from interspecific correlations between population densities, survival and reproduction of the two species during a 25-year demographic study in bluegrass and tallgrass.

**5.** We conclude that food resources and interspecific competition do not play a major role in driving the dynamics of M. *ochrogaster* and *M. pennsylvanicus* populations in our study sites.

*Key words*: demography, food resources, interspecific competition, *Microtus ochrogaster, Microtus pennsylvanicus*, voles

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## Introduction

Food availability is presumed to have substantial influence on the dynamics of arvicoline (microtine) rodent populations. Higher levels of food resources, whether naturally occurring or experimentally supplemented, have been shown to increase population densities or amplitudes of fluctuation (Meserve 1971; Cole & Batzli 1978; Taitt & Krebs 1981; Desy & Thompson 1983; Ford & Pitelka 1984; Boutin 1990; Batzli & Lesieutre 1991; Hall *et al*. 1991). Greater survival, higher reproduction, more rapid body growth, higher body mass, more rapid reproductive maturation, and increased immigration have been attributed to greater success of populations in high food habitats (Cole & Batzli 1978, 1979; Taitt & Krebs 1981, 1983; Desy & Thompson 1983; Desy & Batzli 1989). Most studies involving food supplementation, however, have found that increased levels of food do not substantially alter the pattern of population dynamics (Krebs & DeLong 1965; Cole & Batzli 1978; Desy & Thompson 1983; Boutin 1990). Populations in supplementally fed sites increase and decline in approximate synchrony with populations in control sites. Results of recent studies also indicate that food resources may not be the primary factor responsible for population success of a species (Lin & Batzli 2001; Getz *et al*. In Review a).

Most evidence for the influence of food on population dynamics of arvicoline rodents comes from comparison of population dynamics in supplementally fed and control sites in the same habitat. Such experimental designs presume that food is a limiting factor in the habitat studied, and that control sites provide less food than is required for maximum population success of the species. Interactions between species with similar food requirements may restrict food availability to individual species (Haken & Batzli 1996). This may adversely affect survival and reproduction of competing species, especially in habitats where food is limited. Thus, the response of a population to food shortages can be influenced by presence or absence of a competing species.

As a part of a long-term study of population dynamics of the prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus*, (Getz *et al*. 2001), we conducted manipulative studies to test the role of food resources and interspecific competition on the dynamics of these two sympatric species of voles. Experimental manipulations involved either supplemental feeding of populations in habitats with presumed marginal and low food resources for both species, or the removal of one of the species from marginal and low food sites to reduce interspecific competition.

## Study sites and methods

### STUDY SITES

The study sites were located in the University of Illinois Biological Research Area (“Phillips Tract”) and Trelease Prairie, both 6 km NE of Urbana, Illinois (40°15’N, 88°28’W). During the 25-year study, populations of *M. ochrogaster* and *M. pennsylvanicus* were monitored in three habitats: restored tallgrass prairie (March 1972--May 1997), bluegrass, *Poa pratensis* (January 1972--May 1997) and alfalfa, *Medicago sativa* (May 1972--May 1997). Tallgrass prairie was the original habitat of both species in Illinois and bluegrass, a species introduced to Illinois, represents one of the more common habitats in which the two species can be found today. Tallgrass is a very low food habitat, while bluegrass provides an intermediate food source (Thompson 1965; Cole & Batzli 1979; Lindroth & Batzli 1984). Alfalfa is an atypical habitat that provides exceptionally high-quality food for both species (Cole & Batzli 1979; Lindroth & Batzli 1984). Thus, manipulative studies were conducted in bluegrass and tallgrass, where food was presumed to be a limiting factor for the two species.

The tallgrass manipulations were conducted in study sites in two restored tallgrass prairies: one located in Trelease Prairie, the other in Phillips Tract (Getz *et al.* 2001). Trelease Prairie, established in 1944, was bordered by a mowed lawn, cultivated fields, forbs and shrubs, and a macadam county road. Relative abundances of plants in Trelease Prairie were as follows: big bluestem, *Andropogon gerardii* (17%); bush clover, *Lespedeza cuneata* (16%); ironweed, *Vernonia* (12%); Indian grass, *Sorghastrum nutans* (10%); milkweed, *Asclepias* (9%); goldenrod, *Solidago* (9%); *P. pratensis* (5%); switch grass, *Panicum* (5%); blackberry, *Rubus* (2%); little bluestem, *A. scoparius* (2%); about 10 other species with relative abundances of <1% (Getz *et al.* 1979).

The tallgrass prairie in the Phillips Tract was established in 1968. This site was bordered on one side by an abandoned field and by cultivated fields on the other three sides. When the Phillips Tract site was first trapped in September 1977, prairie vegetation was well established. Lindroth & Batzli (1984) recorded relative abundances of the most prominent plant species in that site: *A. gerardii*, (38%); *Lespedeza cuneata* (25%); Beard tongue foxglove, *Penstemon digitalis* (16%); and *S. nutans* (19%). All other species represented <1% relative abundance. Both prairies were burned during the spring at 3-4-year intervals to control invading shrubs and trees. Study sites were trapped in Trelease Prairie or Phillips Tract, depending upon requirements of the overall study (Getz et al. 1987).

The bluegrass study sites were established within a former bluegrass pasture located in Phillips Tract (Getz et al. 2001). The pasture was released from grazing in June 1971; dense vegetative cover existed by autumn 1971. Relative abundances of plants in the manipulative sites were: *P. pratensis* (70%); dandelion, *Taraxacum officinale* (14%); wild parsnip, *Pastinaca sativa* (4%); goatsbeard, *Tragopogon* (3%); about 20 other species with relative abundance of $\leq$1% (Getz *et al*. 1979).

To reduce successional changes, especially invading forbs, shrubs and trees, bluegrass sites were mowed in their entirety during late summer every 2-3 years. A rotary mower was set to cut the vegetation about 25 cm above the surface. This height suppressed growth of the invading forbs and woody vegetation, but left the bluegrass uncut.

### PROCEDURES

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

Traps were set in the afternoon and checked at about 0800 h and 1500 h on the following three days. All animals were toe-clipped, $\leq$2 toes on each foot, at first capture for individual identification. Although toe clipping no longer is a recommended method of marking animals, during most of the time of the study, few alternative methods were available. Ear tags were available, but owing to frequent loss of tags, toe clipping was deemed a more effective means of marking individuals. The field protocol, including use of toe clipping, was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study. The committee approved the field protocol, based on University and Federal guidelines, as well as those recommended by the American Society of Mammalogists, in effect at the time.

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

We estimated the density of voles for each trapping session using the minimum number alive method (MNA, Krebs 1966, 1999). Previously marked individuals not captured in a given trapping session, but trapped in a subsequent session, were considered to have been present during sessions in which they were not captured. Ssince we utilized prebaited multiple-capture live-traps checked twice daily for 3 days each session, our capture efficiency was very high. Of animals estimated to be present, 92% of *M. ochrogaster* individuals and 91% of *M. pennsylvanicus* individuals actually were captured each session. For additional details regarding procedures and trapping efficiency, see Getz et al. (2001).

## MANIPULATIVE STUDIES

*Supplemental feeding.* A 0.5 ha bluegrass study site was supplementally fed from June 1977 through December 1983. An adjacent 0.8 ha bluegrass site, separated from the supplementally fed site by a 15 m closely mown area, served as the control (Getz *et al*. 1987). These were the same sites utilized by Cole & Batzli (1978) from May 1975-November 1976. A 0.5 ha tallgrass site at the east end of the tallgrass prairie in Phillips tract (Getz et al. 2001) was supplementally fed from September 1977 through May 1987. A similarly sized site at the west end of the prairie, 150 m from the supplementally fed site, served as the control. Both *M. ochrogaster* and *M. pennsylvanicus* occurred in the supplementally fed and control sites through May 1984. From September 1984 through March 1987, *M. pennsylvanicus* were removed from both the supplementally fed and control sites in tallgrass habitat.

Feeding stations, consisting of 0.5 liter glass bottles, were placed at each trapping station. Purina rabbit chow (No. 5321), a high quality diet for both *M ochrogaster* and *M. pennsylvanicus* (Cole & Batzli 1979), was used as supplemental food. The bottles were checked twice weekly and refilled as necessary to ensure food was present in them and in good condition at all times.

*Interspecific interaction.* We examined the effects of one species on the other in bluegrass and tallgrass. All *M. ochrogaster* were removed from a 1 ha bluegrass site from May 1977 through May 1987. *M. pennsylvanicus* were removed from another 1 ha bluegrass site from May 1977 through May 1997. Because *M. ochrogaster* populations were very low and *M. pennsylvanicus* very high most of the time in tallgrass, only effects of *M. pennsylvanicus* on *M. ochrogaster* were tested in tallgrass. We removed *M. pennsylvanicus* from a 0.5 ha tallgrass site at the west end of the Phillips tract tallgrass prairie from September 1984 through May 1997. From January 1981 through November 1983, *M. pennsylvanicus* also were removed from a 0.67 ha tallgrass site in Trelease prairie (Getz *et al*. 1987). Removed animals were released on the opposite side of an Interstate highway, approximately 1 km from the study sites.

We compared population density, survival, persistence of young, proportion of reproductive females, and number of immigrants in the sites where each species was alone with the sites where both species were present.

We also utilized the 25-yr data set to test for correlations between population density of one species and population density, monthly survival rates, persistence of young, and proportion of reproductive females of the other species. Detailed analyses were limited to bluegrass because *M. ochrogaster* was either absent or in very low numbers most of the time in tallgrass. Even in bluegrass, each species was often absent or at very low densities for extended periods of time and thus we conducted additional analyses limited to periods when population densities of the potentially “suppressing” species were at or above the 25-year mean for bluegrass: *M. ochrogaster*, 18/ha; *M. pennsylvanicus*, 14/ha (Getz *et al.* 2001). Effects of *M. ochrogaster* on *M. pennsylvanicus* in tallgrass were examined for the few periods during which densities of *M. ochrogaster* were above the 25-yr mean for tallgrass (8/ha).

### DATA ANALYSIS

Those demographic variables deemed most important with respect to population demography included survival, reproduction, persistence of young, and number of immigrants. Monthly survival was defined as the proportion of the animals present one month that survived to the next month. Animals that weighed $\leq$29 g when first captured were presumed to have been born on the study site since the last trapping session. We calculated persistence of these animals as the time elapsed from first capture to their disappearance from the site. We also calculated for each month the proportion of adult ($\geq$30 g) females that had been recorded as reproductive (open vulva, lactating or pregnant). Unmarked adult animals caught during a given month were presumed to have been born elsewhere and to have immigrated into the study site since the previous trapping session (Dueser *et al*. 1981, Tamarin 1984).

Individuals occupying higher quality habitats are expected to be in better condition and to have higher body mass than those occupying lower quality habitats where food is in short supply. Thus, we used body mass as an indirect indicator of the quality of animals in supplementally fed and control sites. We limited our body mass comparisons to adult males ($\geq$30 g) to avoid bias from variation in the proportion of population comprised of young animals and from variation in reproductive status of adult females.

### STATISTICAL ANALYSES

Because most of the variables did not meet the requirements for normality (population densities and demographic variables were non normal at the 0.05 level; Kolmogorov-Smirnov test, Zar 1999), all variables were log-transformed. Variables that included “zeros” were log (X+1)-transformed because logarithm of zero is not defined. Such transformations allowed us to test for differences using analysis of variance (ANOVA), Pearson’s correlation analyses or independent-sample t-tests. When degrees of freedom (df) for t-tests are given in whole numbers, variances are equal (Levene’s test for equality of variances). When variances were not equal, df is given to one decimal place. SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) was used for all statistical analyses.

## Results

### INFLUENCE OF SUPPLEMENTAL FEEDING

### *Microtus ochrogaster*

*Bluegrass*. The patterns of population dynamics of *M. ochrogaster* were generally similar in the supplementally fed and control sites ( Fig. 1). Although peak densities of the three population cycles were higher in the supplementally fed than the control site (Fig. 1), there was no difference in mean monthly population densities in the two sites (Table 1). Total survival was marginally higher in the supplementally fed site than in the control, while persistence of young and number of immigrants in the two sites did not differ (Table 1). The proportion of reproductive females was more than twice as high in the supplementally fed site than in the control site (Table 1). Male body mass was greater in the supplementally fed site than in the control site (39.2±0.5 g and 36.6±0.4 g, respectively; $t$=3.752, df=219, $P$= 0.001). Population densities of *M. pennsylvanicus* were similar in the two sites throughout most of the study (Fig. 1), and thus were unlikely to have influenced the effects of additional food availability on the *M. ochrogaster* population.

*Tallgrass*. *Microtus ochrogaster* was either absent or in very low numbers in both supplementally fed and control sites throughout the study (Fig. 2). Generally, when *M. ochrogaster* was present, there were more individuals of this species in the control site than in the supplementally fed site, especially late 1982-late 1983. Population densities of *M. pennsylvanicus* were very high in both the supplementally fed and control sites throughout the study (Fig. 2). A suppressing effect of *M. pennsylvanicus* on *M. ochrogaster* in tallgrass (see below) most likely contributed to the low numbers of *M. ochrogaster* in the two sites. When *M. pennsylvanicus* were removed from both the supplementally fed and control sites, however, population densities of *M. ochrogaster* were still lower in the supplementally fed site than in the control site (Fig. 3). There was no difference in male body mass in supplementally fed and control sites (40.6±0.7 g and 40.1±0.5 g, respectively; $t$=0.520, df=22, $P$=0.603). Because of the very low numbers in the main manipulated site and the short duration of the removal study, we did not attempt analyses of demographic responses of *M. ochrogaster* to supplemental feeding in tallgrass.

### *Microtus pennsylvanicus*

*Bluegrass*. Amplitudes of fluctuation of *M. pennsylvanicus* were generally higher in the control than in the supplementally fed site (Fig. 1). Although population densities and monthly survival were also higher in the control site than in the supplementally fed site, we found no differences between the sites in the persistence of young, proportion of reproductive females or number of immigrants (Table 1). Male body mass also did not differ between the supplementally fed and control sites (40.8±0.8 g and 40.6±0.4 g, respectively; *t*=0.500, df=471, *P*=0.618). Population densities of *M. ochrogaster* were sufficiently similar in the two sites (Fig. 1) so as not to be a factor in influencing effects of supplemental feeding on populations of *M. pennsylvanicus*.

*Tallgrass*. *M. pennsylvanicus* populations in supplementally fed and control tallgrass sites were erratically high at all times, with no indication of distinct population cycles (Fig. 2; Getz *et al.* 2001). Population densities in the supplementally fed tallgrass site were higher than those in the control site, and this difference approached significance (Table 1). There were no differences in either overall survival or persistence of young between the two sites, but proportion of females reproductive and number of immigrants were greater in the supplementally fed site (Table 1). Further, male body mass was higher in the supplementally fed site than in the control site (42.0±0.4 g and 39.4±0.3 g, respectively; *t*=5.849, df=820.8, *P*<0.001).

### EFFECTS OF INTERSPECIFIC COMPETITION: REMOVAL EXPERIMENTS

#### *Effect of Microtus pennsylvanicus upon M. ochrogaster*

*Bluegrass*. Population dynamics of *M. ochrogaster* in bluegrass were similar in the control site and the site from which *M. pennsylvanicus* was removed (Fig. 4). Population densities did not differ between control and removal sites (Table 2). For much of the time from 1982 through the end of the study, *M. pennsylvanicus* numbers were very low in bluegrass (Fig. 4). Comparisons were, therefore, made for periods when population density of *M. pennsylvanicus* was ≥14/ha (i.e., above the 25-yr mean density for bluegrass) in the control sites. Again, the difference in population densities of *M. ochrogaster* between control

(5.1±1.8/ha) and removal sites was not significant (6.7±1.8/ha) sites (*t*=1.316. df=148, *P*=0.190).

Although overall monthly survival of *M. ochrogaster* was significantly higher when alone than when in the presence of *M. pennsylvanicus*, persistence of young on the two study sites did not differ (Table 2). The proportion of reproductive females and the number of immigrants were greater where *M. pennsylvanicus* was present (Table 2).

A significant positive correlation existed between the proportion of reproductive females of *M. pennsylvanicus* and *M. ochrogaster* in the control site (*r*=0.537, N=34, *P*=0.001). The correlation between survival of the two species in the control site approached significance (*r*=0.316, N=37, *P*=0.057).

*Tallgrass*. Overall, amplitudes of fluctuation of *M. ochrogaster* were higher when the species was alone than when in the presence of *M. pennsylvanicus* (Figs. 5, 6). Population densities and number of immigrants were higher when the species was alone than when with M. pennsylvanicus (Table 2). However, monthly survival, persistence of young, and proportion of reproductive females did not differ between the control and removal sites (Table 2).

### *Effect of Microtus ochrogaster on M. pennsylvanicus*

Detailed interaction effects of *M. ochrogaster* on *M. pennsylvanicus* population densities were determined only for bluegrass habitat. Because *M. pennsylvanicus* densities were high in tallgrass at all times (Fig. 7) it appeared that there was no suppressing effect of *M. ochrogaster* on *M. pennsylvanicus* in this habitat.

When densities of *M. ochrogaster* in bluegrass were low, *M. pennsylvanicus* typically were higher in the control than where alone

(Fig. 8). During periods of moderately high densities of *M. ochrogaster* in the control site (late 1980-early 1982; late 1982-early 1984; late 1984-early 1986), population densities of *M. pennsylvanicus* were essentially the same in the two sites or higher where the two species occurred together (Fig. 8). Only during a 7-month period of very high densities of *M. ochrogaster* (>50/ha) in 1985 were numbers of *M. pennsylvanicus* lower where the two species were present than where alone (Fig. 8). Overall, *M. pennsylvanicus* population density in bluegrass was higher when in the presence of *M. ochrogaster* than when alone (Table 2). There were no differences in monthly survival, persistence of young, proportion of reproductive females or number of immigrants of *M. pennsylvanicus* in the control and removal sites (Table 2).

### CORRELATIVE STUDY: ASSESSMENT OF SPECIES INTERACTIONS BASED ON 25-YR DATA SET

There was no correlation between population densities of the two species in bluegrass during the 25-yr study (Fig. 9; $r$=0.040, N=273, $P$=0.454). Although there was a negative correlation between survival of *M. ochrogaster* and population density of *M. pennsylvanicus*, there was no correlation between proportion reproductive female *M. ochrogaster* and population density of *M. pennsylvanicus* ($r$=-0.176, N=202, $P$=0.012 and $r$=0.006, N=161, $P$=0.943, respectively). Population density of *M. ochrogaster* was not correlated with either survival (r=0.049, N=196, $P$=0.494) or reproduction of *M. pennsylvanicus* ($r$=0.002, N=162, $P$=0.976). Proportion of *M. pennsylvanicus* reproductively active was significantly correlated with that of *M. ochrogaster* ($r$=0.508, N=101, $P$< 0.001), but survival of the two species was not correlated ($r$=0.008, N=148, $P$=0.924).

Population densities, survival and persistence of young of *M. ochrogaster* were significantly lower when *M. pennsylvanicus* densities were above their 25-yr mean in bluegrass (14/ha) than when such densities were below the 25-yr mean (Table 3). There was no difference in the proportion of reproductive female *M.* ochrogaster when population densities of *M. pennsylvanicus* were above and below the 25-yr means. Population densities, survival, persistence of young, and proportion of reproductive females of *M. pennsylvanicus* were not lower when population densities of *M. ochrogaster* were above the 25-year mean of 18/ha than when densities were below the mean.

Comparison of population densities of *M. pennsylvanicus* in tallgrass when densities of *M. ochrogaster* were below and above the 25-yr mean (8/ha) showed densities of *M. pennsylvanicus* to be higher when *M. ochrogaster* was greater than 8/ha (Fig. 7; 26.8±1.8 and 41.5±3.1, respectively; $t$=4.279, df=282, $P$<0.001). Only during the exceptionally high population densities of *M. ochrogaster* in tallgrass during 1989-1990 was there an indication of possible suppression of *M. pennsylvanicus* (Figs. 5 and 7). However, during this 7-month period, there was no difference in survival of *M. pennsylvanicus* in contrast to other months (0.608±0.142 and 0.703±0.491, respectively; $t$=1.170, df=246, $P$=0.243)

## Discussion

Supplemental feeding resulted in mixed responses with respect to species and habitat. Although amplitudes of fluctuation and peak densities of *M. ochrogaster* population cycles were higher in the supplementally fed than in the control bluegrass site, mean population densities did not differ between the two sites. Further, the basic pattern of fluctuation was the same in the two sites. The most dramatic response to supplemental feeding in this species was increased reproduction. The proportion of reproductive females was twice as great in the supplementally fed site as compared to the control site. Body mass of adult males was greater in the supplementally fed site than in the control site, and survival rates were 11% higher in the supplementally fed area. The combination of greater reproduction and slightly higher survival resulted in higher peak densities during population cycles, but did not influence densities at other times.

*Microtus pennsylvanicus* did not display a positive response to supplemental feeding in bluegrass. Indeed, population densities were typically higher in the control site than in the supplementally fed site, and survival rates were significantly higher in the control. Further, we found no differences between the two sites in persistence of young, proportion of reproductive females, number of immigrants, or male body mass.

Our finding that neither species displayed major positive population density responses to supplemental feeding in bluegrass suggests either that natural food levels were sufficient for population success of both species or that competition for food did not exist. Our results are consistent with those reported for *M. ochrogaster* by Cole and Batzli (1978) from the same study sites; amplitudes of fluctuation were higher in the supplementally fed site than in the control, but the patterns of fluctuation were similar in the two sites. Cole and Batzli (1978) removed the few *M. pennsylvanicus* that immigrated into their sites (the latter species was colonizing our study region during their study; Getz *et al.* 1978). Thus, they did not obtain data regarding effects of supplemental feeding on either *M. pennsylvanicus* or competition for food between the two species.

Results of supplemental feeding in tallgrass suggest food availability is not the primary factor limiting population density of either species in this habitat. *M. ochrogaster* populations were very low in both the supplementally fed and control sites; no response to supplemental feeding was observed. This may have been related, in part, to competition from *M. pennsylvanicus*, which was present in high densities in both sites. However, a short term study in which *M. pennsylvanicus* was removed from both sites, did not result in higher densities of *M. ochrogaster* in the supplementally fed site than in the control site. There were too few data available to test for differences in survival or reproduction of *M. ochrogaster* in supplementally fed and control sites. Male body mass did not differ between the 2 sites.

*Microtus pennsylvanicus* displayed slightly higher densities in the supplementally fed tallgrass site than in the control site; this difference approached statistical significance. Proportion of reproductive females and number of immigrants were significantly greater, as was male body mass, in the supplementally fed than in the control site. There were no differences in survival or persistence of young in the two sites.

From these results, food does not appear to be the primary factor influencing population density of either species in bluegrass or tallgrass. The slight response of *M. ochrogaster* and lack of response by *M. pennsylvanicus* to supplemental food in bluegrass are consistent with our prior conclusions that bluegrass provides adequate food for *M. pennsylvanicus* and marginal food for *M. ochrogaster* (Getz *et al*. In Review a,b). The results of supplemental feeding in tallgrass are not consistent with presumed food availability for the two species in this habitat. While tallgrass is presumed to be low in dicots, the preferred food for both species, *M. pennsylvanicus* can utilize monocots (Haken & Batzli 1996). That it makes use of monocots may account for only a modest response of *M. pennsylvanicus* to supplemental feeding in tallgrass. However, *M. ochrogaster*, for which preferred food was very low, did not display a positive response to supplemental feeding.

*Microtus pennsylvanicus* suppressed population densities of *M. ochrogaster* in tallgrass. This negative effect may have over-ridden the positive effect of additional food. That a positive response to food was not observed when *M. pennsylvanicus* was removed from both the supplementally fed and control sites may have resulted from the short time span of the study. *M. ochrogaster* were present in high numbers in both sites only one of the three years.

The modest positive responses to supplemental feeding by *M. ochrogaster* (bluegrass) and *M. pennsylvanicus* (tallgrass) appear to have resulted mainly from higher reproduction. Greater body mass of adult males, perhaps an indication of better quality animals, also occurred in response to supplemental food. These results suggest that improvements in the quality of animals may enhance reproduction, but not survival.

Population densities of the two species of voles in bluegrass were not correlated throughout the 25-year general study. Although higher population densities of *M. pennsylvanicus* had a significant negative effect on survival of *M. ochrogaster*, there was no correlation between population density of *M. pennsylvanicus* and reproduction of *M. ochrogaster*. Further, population densities of *M. ochrogaster* were not correlated with survival or reproduction of *M. pennsylvanicus*. Krebs (1977) found no suppressive interaction between these two species in open populations in Indiana.

There was a positive correlation between reproduction of *M. pennsylvanicus* and *M. ochrogaster* in bluegrass. This suggests that what is good for reproduction of *M. pennsylvanicus* is also good for reproduction of *M. ochrogaster*. In contrast, there was no correlation between survival of the two species. These latter results indicate that the two species may be subject to different mortality factors.

Results of the removal experiments in bluegrass did not agree completely with the correlational studies of interactions between the two species, based on the 25-yr data set. Densities of *M. ochrogaster* were similar when alone and when with *M. pennsylvanicus*, including periods when densities of the latter species were above 14/ha (the mean density of *M. pennsylvanicus* in bluegrass). Survival and persistence of young were lower in the presence of *M. pennsylvanicus*, but reproduction was higher. Higher reproduction in the control site may have offset effects of reduced survival. Population densities of *M. pennsylvanicus* in bluegrass also were similar when alone and when in the presence of *M. ochrogaster*, except at very high ($\geq$ 50/ha) densities of the latter species. Survival, persistence of young, reproduction, and number of immigrants were similar in the removal and control sites. As for the general study, there was a positive correlation between reproduction of *M. pennsylvanicus* and *M. ochrogaster* in the control sites, while the correlation of survival between the two species only approached significance.

*Microtus pennsylvanicus* exerted a strong suppressing effect on mean population densities of *M. ochrogaster* in tallgrass. However, survival, persistence of young and reproduction did not differ between the site where *M. ochrogaster* was alone and the control site; only the number of immigrants was greater where *M. ochrogaster* was alone. We detected no effect of presence of *M. ochrogaster* on demography of *M.*

*pennsylvanicus* in tallgrass, except for a 7-month period of exceptionally high densities ($\geq$ 50/ha),.

Results of this study agree with those of previous studies (e.g., (Cole & Batzli 1978, 1979; Taitt & Krebs 1981, 1983; Desy & Thompson 1983; Desy & Batzli 1989; Getz *et al*. In Review a) in suggesting that food is not the primary factor responsible for abundance of arvicoline rodents in given habitats. Modest positive responses to addition of food were noted for *M. ochrogaster* in bluegrass, which provides marginal food for this species. However, when in competition with *M. pennsylvanicus*, which prefers similar food plants, the major negative effect was lower survival of *M. ochrogaster*. Reproduction, presumed to be more reliant on food availability than is survival, was not affected by higher densities of *M. pennsylvanicus*. Additional food in bluegrass did not elicit a positive response by *M. pennsylvanicus*, indicating food was not a limiting factor in this habitat.

In tallgrass, *M. pennsylvanicus* displayed only a minor positive response to additional food, suggesting the importance of monocots in the diet of this species (Haken & Batzli 1996). The lack of response of *M. ochrogaster* to supplemental food in tallgrass agrees with our previous conclusions that mortality from predation, not low food availability, is the primary factor resulting in low densities in this habitat (Getz *et al*. In Review a, b). When *M. ochrogaster* did achieve high population densities in tallgrass, these periods normally coincided with periods of high densities of *M. pennsylvanicus* (except as noted above). This further suggests something other than competition for food was responsible for the generally low population densities of *M. ochrogaster* in this habitat.

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Table 1. Effects of supplemental feeding on the demography of *M. ochrogaster* and *M. pennsylvanicus* in bluegrass and *M. pennsylvanicus* in tallgrass. Pop density, No./ha; 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 ± SE) of females reproductive; Immigrants, number (mean ± SE) of immigrants per month. See text for definition of variables and statistics. Values within a column with different superscripts differ significantly at the 0.05 level (Tukey's HSD test).

| | Pop density | Survival | Persistence | % Reproductive |
|---|---|---|---|---|
| Bluegrass | | | | |
| ***M. ochrogaster*** | | | | |
| Supplemental | 11.5 ± 1.9 | 0.468 ± .043 | 1.81 ± .20 | 0.798 ± .053 |
| Control | 8.8 ± 1.3 | 0.358 ± .039 | 1.64 ± .11 | 0.358 ± .039 |
| *t*; df | -0.171; 152.256 | 2.014; 90 | 0.583; 165 | 6.250; 89 |
| **P** | 0.865 | 0.047 | 0.561 | <0.001 |

Table 1 (Cont.)

| | | | | |
|---|---|---|---|---|
| ***M. pennsylvanicus*** | | | | |
| Supplemental | 22.3 ± 3.2 | 0.491 ± .035 | 2.03 ± .17 | 0.660 ± .057 |
| Control | 31.3 ± 2.7 | 0.572 ± .024 | 2.11 ± .11 | 0.656 ± .037 |
| *t;* df | -4.160; 138.323 | -2.152; 121 | -0.644; 396 | -0.167; 115 |
| **P** | <0.001 | 0.033 | 0.520 | 0.868 |
| Tallgrass | | | | |
| *M. pennsylvanicus* | | | | |
| Supplemental | 60.0 ± 3.7 | 0.637 ± .020 | 2.64 ± .18 | 0.600 ± .036* |
| Control | 46.9 ± 3.5 | 0.639 ± .020 | 2.59 ± .15 | 0.485 ± .044 |
| *t*; df | 1.907; 160 | 0.03; 149 | -0.163; 417 | 2.23; 134.65 |
| **P** | 0.058 | 0.979 | 0.870 | 0.027 |

Table 2. Effects of the presence of one species of vole on demography of the other species in bluegrass and tallgrass. See Table 1 and text for definition of variables and statistics.

| | Pop density | Survival | Persistence | Reproductive |
|---|---|---|---|---|
| Bluegrass | | | | |
| *M. ochrogaster* | | | | |
| With *M. penn.* | 16.4 ± 1.8 | 0.445 ± .023 | 1.95 ± .10 | 0.758 ± .033 |
| Alone | 13.4 ± 1.7 | 0.546 ± .023 | 1.96 ± .10 | 0.650 ± .033 |
| *t*; df | 1.434; 480 | 3.329; 294.1 | 0.141; 665 | 2.396; 249.74 |
| **P** | 0.152 | 0.001 | 0.888 | 0.017 |
| ***M. pennsylvanicus*** | | | | |
| With *M. ochr.* | 23.1 ± 2.1* | 0.571 ± .02 | 2.14 ± .10 | 0.602 ± .037 |
| Alone | 13.8 ± 1.4 | 0.589 ± .020 | 2.22 ± .12 | 0.560 ± .041 |
| *t*; df | 1.996; 218.5 | 0.284; 201.2 | 0.086; 6 | 0.858; 2 |
| **P** | 0.047 | 0.777 | 0.931 | 0.392 |

Table 2 (Cont.)

| | | | | |
|---|---|---|---|---|
| Tallgrass | | | | |
| ***M. ochrogaster*** | | | | |
| With *M. penn.* | 7.8 ± 1.6 | 0.474 ± .040 | 2.32 ± .29 | 0.641 ± .073 |
| Alone | 22.8 ± 3.8* | 0.560 ± .034 | 2.27 ± .14 | 0.661 ± .052 |
| *t*; df | 3.426; 219.3 | 1.570; 61.1 | 0.356; 287 | 0.320; 82 |
| *P* | 0.001 | 0.121 | 0.722 | 0.749 |

Table 3. Effects of presence of one species of vole on the demography of the other species in bluegrass when population densities were higher and lower than the mean density over the 25 years of the study. See Table 1 and text for definition of variables.

| | Pop density | Survival | Persistence | Reproductiv |
|---|---|---|---|---|
| *M. ochrogaster* | | | | |
| *M. penn.* > mean | 9.0 ± 1.7 | 0.297 ± .034 | 1.67 ± .07 | 0.748 ± .05 |
| *M. penn.* < mean | 18.9 ± 2.3 | 0.528 ± .020 | 2.09 ± .06 | 0.725 ± .02 |
| *t*; df | 2.927; 217.1 | -5.733; 95.122 | -2.830; 436.0 | 0.350; 188 |
| **P** | 0.004 | <0.001 | 0.005 | 0.727 |
| *M. pennsylvanicus* | | | | |
| *M. och.* > mean | 9.1 ± 1.5 | 0.625 ± .03 | 2.58 ± .19 | 0.613 ± .06 |
| *M. och.* < mean | 15.7 ± 1.5 | 0.566 ± .020 | 2.00 ± .08 | 0.594 ± .03 |
| *t*; df | 1.28; 153.8 | -1.474; 174 | 3.490; 249.5 | 0.165; 163 |
| **P** | 0.186 | 0.142 | 0.001 | 0.869 |

Fig. 1. Population densities of *Microtus ochrogaster* and *M. pennsylvanicus* in supplementally fed and control bluegrass sites. Both species were present in both sites.

Fig. 2. Population densities of *Microtus ochrogaster* and *M. pennsylvanicus* in supplementally fed and control tallgrass prairie sites. Both species were present in both sites.

Fig. 3. Population densities of *Microtus ochrogaster* in supplementally fed and control tallgrass prairie sites from which all *M. pennsylvanicus* were removed each monthly trapping session. Numbers of *M. pennsylvanicus* that were removed from the two sites each month are also included.

Fig. 4. Population densities of *Microtus ochrogaster* in a bluegrass site from which all *M. pennsylvanicus* were removed each month (*M. ochrogaster* alone) and a control site in which *M. pennsylvanicus* occurred (*M. ochrogaster* control). Population densities of *M. pennsylvanicus* in the control site and the number removed each month from the alone site are also given.

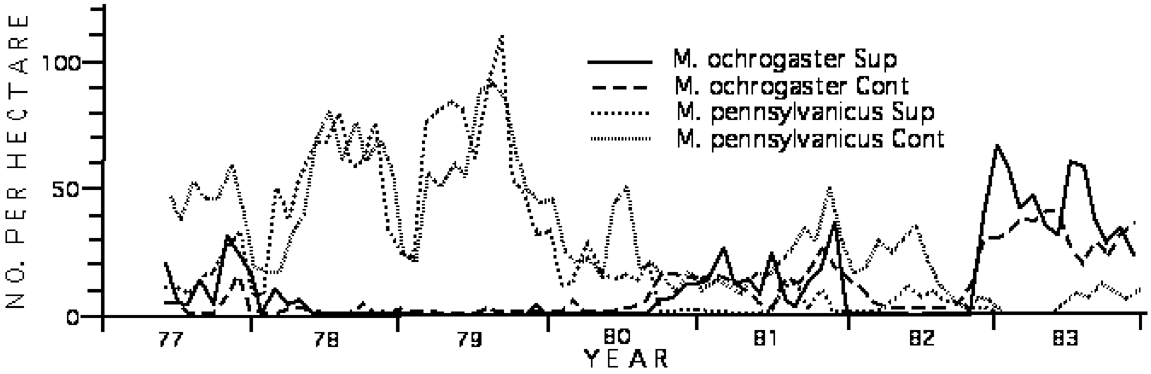
Fig. 5. Population densities of *Microtus ochrogaster* in a tallgrass prairie site from which all *M. pennsylvanicus* were removed each month (*M. ochrogaster* alone) and a control site in which *M. pennsylvanicus* occurred (*M. ochrogaster* control). Population densities of *M. pennsylvanicus* in the control site and the number removed each month from the alone site are also given. Both sites were located in Phillips tract.

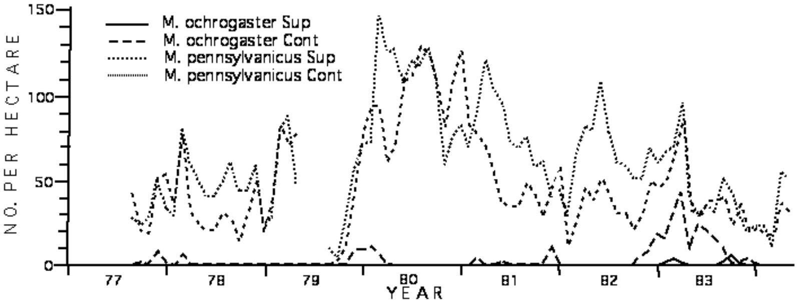
Fig. 6. Population densities of *Microtus ochrogaster* in a tallgrass site in Phillips tract from which all *M. pennsylvanicus* were removed each month (*M. ochrogaster* alone) and a control site in Trelease prairie in which *M. pennsylvanicus* occurred (*M. ochrogaster* control). Population densities of *M. pennsylvanicus* in the control site and the number removed each month from the alone site are also given

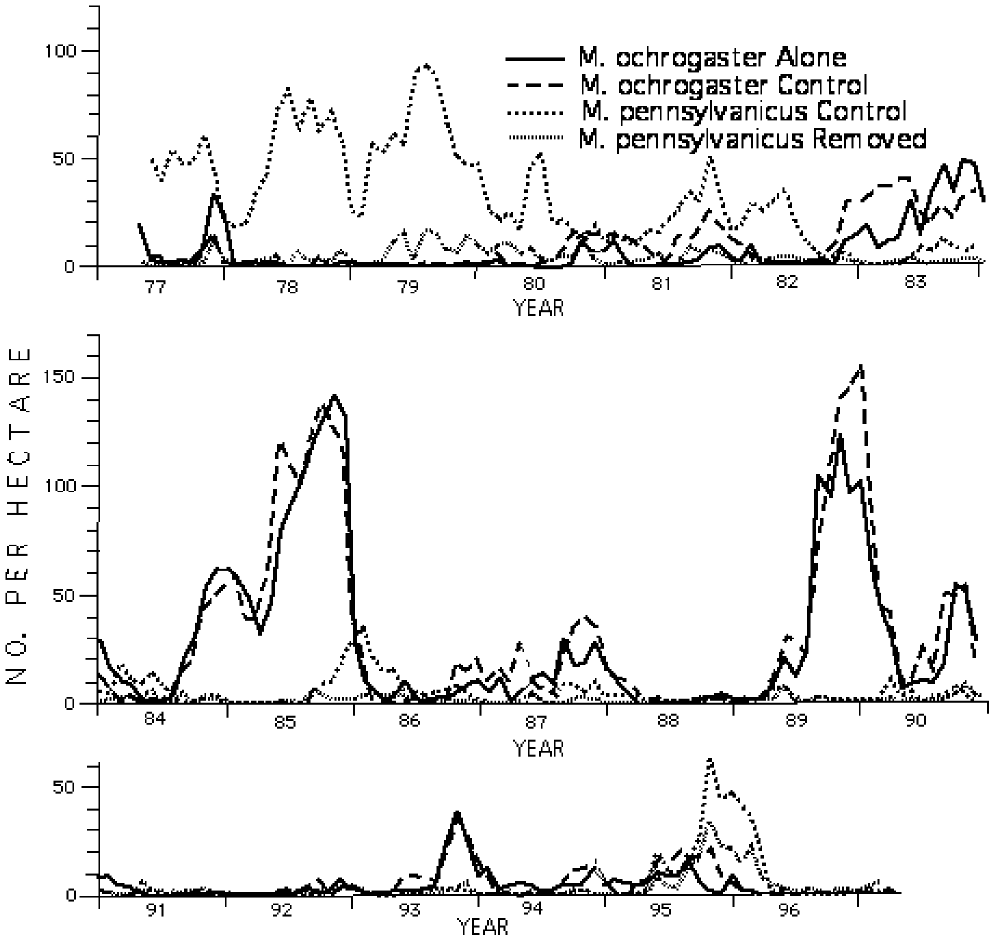
Fig. 7. Population densities of *Microtus ochrogaster* and *M. pennsylvanicus* in tallgrass prairie habitat over a 25-year period. *M. pennsylvanicus* did not colonize the study region until mid 1973.

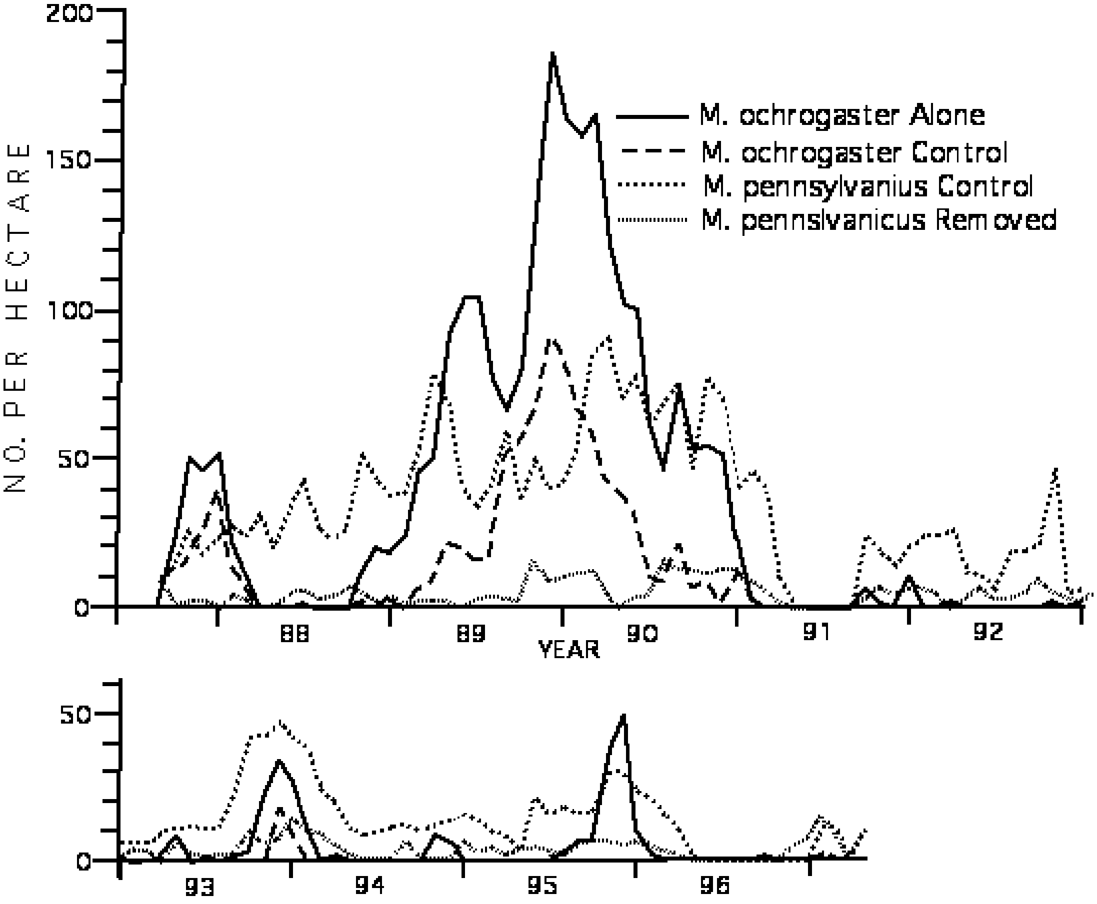
Fig. 8. Population densities of *Microtus pennsylvanicus* in a bluegrass site from which all *M. ochrogaster* were removed each month (*M. pennsylvanicus* alone) and a control site in which *M. ochrogaster* occurred (*M. pennsylvanicus* control). Population densities of *M. ochrogaster* in the control site and the number removed each month from the alone site are also given.

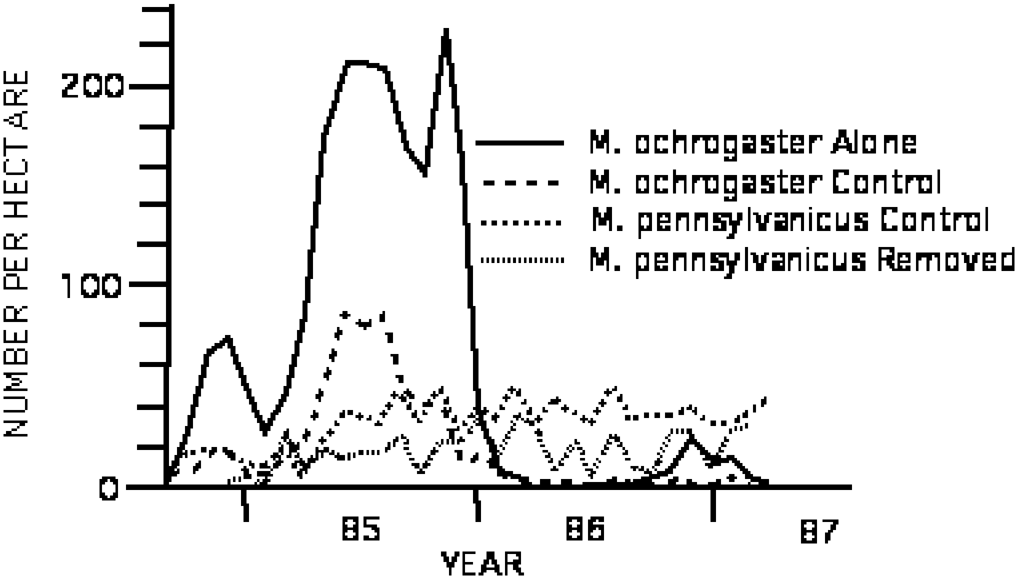
Fig. 9. Population densities of *Microtus ochrogaster* and *M. pennsylvanicus* in bluegrass habitat during a 25-year period. *M. pennsylvanicus* did not colonize the study region until mid 1973.

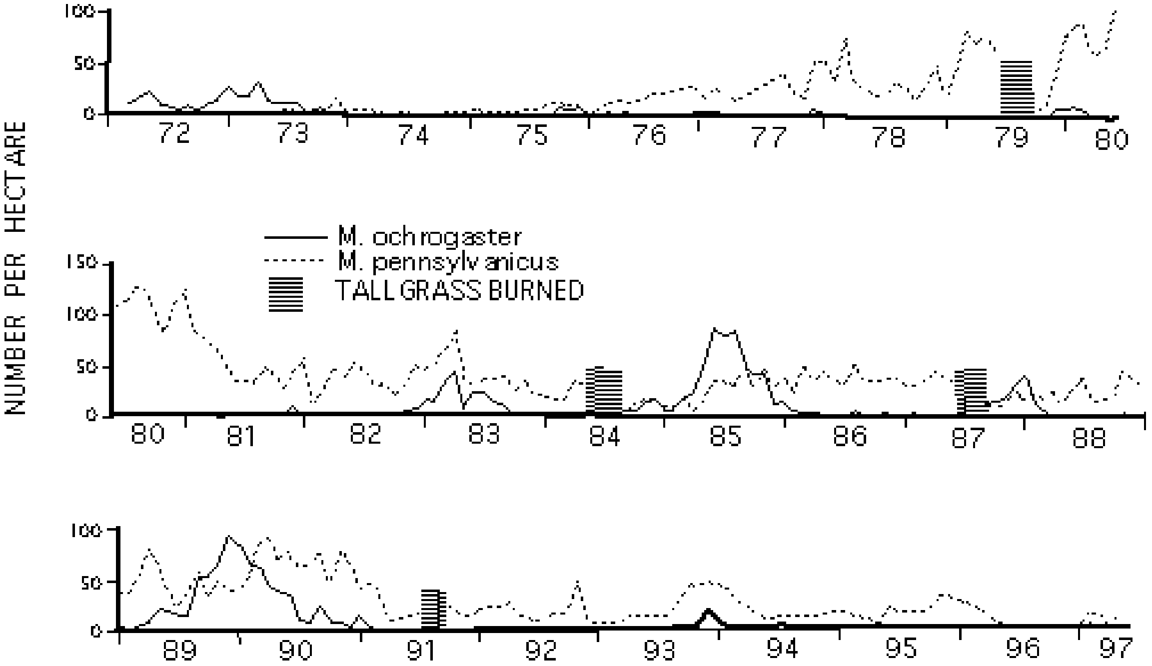

NO. PER HECTARE
0
50
100
M. ochrogaster Sup
M. ochrogaster Cont
M. pennsylvanicus Sup
M. pennsylvanicus Cont
77
78
79
80
81
82
83
YEAR


NO. PER HECTARE
0
50
100
150
M. ochrogaster Sup
M. ochrogaster Cont
M. pennsylvanicus Sup
M. pennsylvanicus Cont
77
78
79
80
81
82
83
YEAR


M. ochrogaster Alone
M. ochrogaster Control
M. pennsylvanicus Control
M. pennsylvanicus Removed
NO. PER HECTARE
0
50
100
150
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
92
93
94
95
96
YEAR


NO. PER HECTARE
200
150
100
50
0
M. ochrogaster Alone
M. ochrogaster Control
M. pennsylvanius Control
M. pennslvanicus Removed
88
89
90
91
92
YEAR
50
0
93
94
95
96


NUMBER PER HECTARE
200
100
0
M. ochrogaster Alone
M. ochrogaster Control
M. pennsylvanicus Control
M. pennsylvanicus Removed
85
86
87
YEAR


NUMBER PER HECTARE
100
50
0
72
73
74
75
76
77
78
79
80
M. ochrogaster
M. pennsylvanicus
TALLGRASS BURNED
150
100
50
0
80
81
82
83
84
85
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88
100
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0
89
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94
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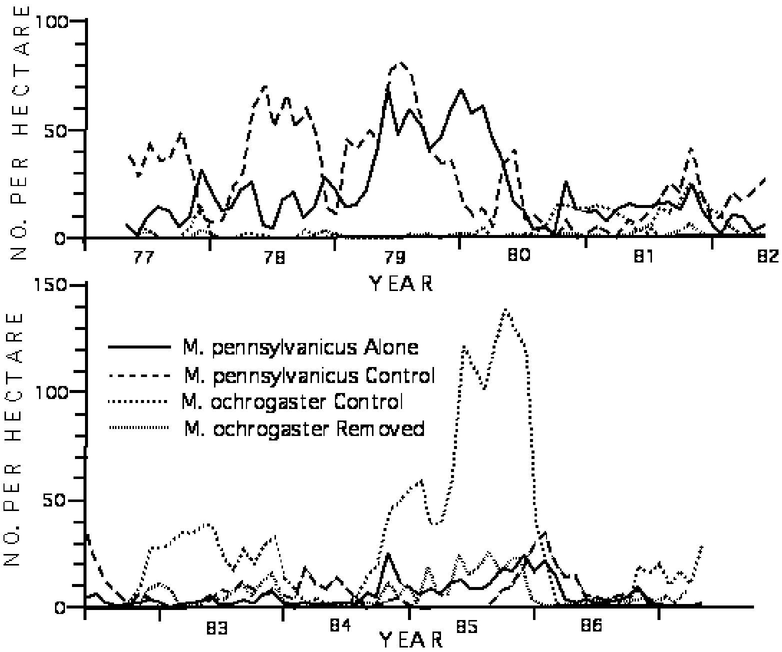
97


NO. PER HECTARE
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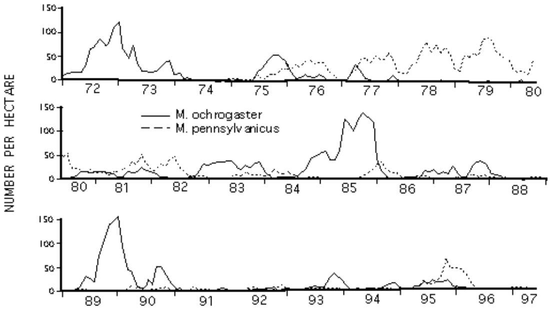
77
78
79
80
81
82
YEAR
NO. PER HECTARE
150
100
50
0
83
84
85
86
YEAR
M. pennsylvanicus Alone
M. pennsylvanicus Control
M. ochrogaster Control
M. ochrogaster Removed


NUMBER PER HECTARE
150
100
50
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72
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74
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78
79
80
M. ochrogaster
M. pennsylvanicus
150
100
50
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