

## Dynamics of sympatric vole populations: influence of interspecific competition<sup>\*</sup>

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**Abstract** We conducted removal experiments in open populations of *Microtus ochrogaster* and *M. pennsylvanicus* to test for potential interspecific competition between coexisting populations in bluegrass and tallgrass prairie in east-central IL, USA. Population densities of *M. ochrogaster* and *M. pennsylvanicus* in bluegrass were not suppressed by presence of the other species. In bluegrass, presence of the other species did not negatively influence monthly survival, persistence of young on the site, reproduction, or number of immigrants of either *M. ochrogaster* or *M. pennsylvanicus*. Although *M. pennsylvanicus* appeared to exert a strong suppressing effect on population densities of *M. ochrogaster* in tallgrass and limited the number of immigrants, survival, persistence of young, and proportion reproductively active female *M. ochrogaster* were not negatively affected by presence of *M. pennsylvanicus*. We conclude that interspecific competition did not play a major role in driving dynamics of coexisting populations of *M. ochrogaster* and *M. pennsylvanicus* in our study sites [Acta Zoologica Sinica 53 (5): 800–811, 2007].

**Key words** Voles, *Microtus ochrogaster*, *Microtus pennsylvanicus*, Demography, Interspecific competition

## 种间竞争对同域分布田鼠种群动态的影响<sup>\*</sup>

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**摘要** 我们对美国伊利诺斯州中东部的蓝草和高草牧场共生的橙腹田鼠 (*Microtus ochrogaster*) 和草原田鼠 (*Microtus pennsylvanicus*) 开放种群进行了去除实验, 以测定潜在的种间竞争。在蓝草草原, 橙腹田鼠和草原田鼠的种群密度不因另一种的存在而受抑制; 同时, 另一种存在的情况下, 相互间对月存活率、青年鼠位置的持久性生殖或迁入鼠数量没有负面影响, 尽管在高草草原, 草原田鼠似乎对橙腹田鼠的种群密度有强烈影响, 并限制了迁入鼠的数量, 但是雌橙腹田鼠的存活率、青年鼠的持久性和生殖活动的比例不因草原田鼠的存在而受影响。总之, 在此研究地点, 种间竞争没有对橙腹田鼠和草原田鼠共存种群的动态起到驱动作用 [动物学报 53 (5): 800–811, 2007]。

**关键词** 田鼠 橙腹田鼠 草原田鼠 种群统计 种间竞争

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Populations of most arvicoline (microtine) rodents have been observed to undergo high amplitude fluctuations in numbers (Krebs and Myers, 1974; Taitt and Krebs, 1985). A species may display different patterns of fluctuation among sites and among years within sites (Getz et al., 2001; Marcström et al., 1990). Although sympatric species may undergo synchronous population fluctuations (Hornfeldt, 1994; Huitu et al., 2004; Korpimäki et al., 2005; Ylönen, 1994), population fluctuations of coexisting species most often are asynchronous (Getz et al., 2001; Krebs et al., 1969).

Survival and reproduction are presumed to be the primary demographic variables responsible for temporal and spatial differences in demography of arvicoline rodents (Batzli, 1992, 1996; Krebs and Myers, 1974; Lin and Batzli, 2001); emigration and immigration do not appear to be important factors influencing population fluctuations (Dueser et al., 1981; Gaines and McClenaghan, 1980; Getz et al., 2005a; Lin and Batzli, 2001; Verner and Getz, 1985). Density-independent factors, including episodes of extreme weather as well as seasonal temperatures and precipitation, may affect survival and reproduction through changes in habitat quality (e.g., food and cover) and increased physiological stress or through direct mortality. Because populations of generalist predators are controlled by factors other than voles alone, mortality from such predators may also be density-independent. Density-dependent factors affecting survival and reproduction may be extrinsic, including specialist predator-prey interactions and habitat degradation from high population densities or intrinsic, e.g., variation in quality of the animals in response to changing social stresses as population density changes (Christian, 1971, 1980; Norrdahl and Korpimäki, 2002).

Interspecific interactions may also affect population densities of coexisting species (Eccard and Ylönen, 2002, 2003a, b; Hansen et al., 1999). Interspecific interactions of coexisting species that result in habitat segregation or depressed population densities (Crowell and Pimm, 1976; Douglass, 1976; Huitu et al., 2004; Morris, 1996; Pimm and Rosenzweig, 1981) involve both decreased survival and reproduction (Crowell and Pimm, 1976; Eccard and Ylönen, 2002, 2003a, 2007; Koivisto et al., 2007). Negative interactions between coexisting species resulting in demographic responses appear to be a result of direct aggressive interaction, rather than indirect interaction, e.g., reduced food availability (Eccard and Ylönen, 2002, 2007).

Prairie voles *Microtus ochrogaster* and meadow voles *M. pennsylvanicus* coexist in several habitats which are dominated by herbaceous plant species in mid-western North America (Getz, 1985). Although grasses are eaten by *M. ochrogaster*, this species cannot subsist successfully on a diet of graminoids alone; forbs are required for successful reproduction and survival (Cole

and Batzli, 1978, 1979; Haken and Batzli, 1996). Whereas *M. pennsylvanicus* preferentially selects forbs over grasses, individuals can subsist and reproduce successfully on graminoids (Haken and Batzli, 1996; Lindroth and Batzli, 1984; Thompson, 1965; Zimmerman, 1965). Both species preferentially select sites where vegetative cover is the greatest; *M. pennsylvanicus*, however, is more reliant than is *M. ochrogaster* on dense cover (Birney et al., 1976; Getz and Hofmann, 1999; Klatt and Getz, 1987; Lin and Batzli, 2001). Getz et al. (2005b) suggested that *M. pennsylvanicus* may be more susceptible than *M. ochrogaster* to predation by raptors and large carnivores. *M. ochrogaster*, on the other hand, may be more susceptible than is *M. pennsylvanicus* to predation by snakes and small carnivores.

Both *M. ochrogaster* and *M. pennsylvanicus* undergo erratic high amplitude population fluctuations (Getz et al., 2001; Krebs et al., 1969). Although the two species may undergo synchronous fluctuations within a site, such synchrony is rare. Getz et al. (2001) recorded 13 population fluctuations of *M. ochrogaster* and five of *M. pennsylvanicus* in alfalfa and 12 population fluctuations of *M. ochrogaster* and nine of *M. pennsylvanicus* in bluegrass in the same sites over a 25 year period; synchronous fluctuations of the two species occurred in only two years, in bluegrass. At other times, the two species coexisted briefly at low densities. Getz et al. (2005c, 2006a, b, 2007) concluded changes in survival to be the primary factor responsible for variation in density and population fluctuations of the two species. A winter decline in reproduction of both species accentuated the rate of decline for those fluctuations peaking in late autumn and winter. Episodes of weather extremes (temperature and precipitation) did not influence population fluctuations of either species (Getz et al., in press, a).

Getz (1962) concluded from laboratory trials that *M. ochrogaster* was slightly aggressively dominant over *M. pennsylvanicus*. Lin and Batzli (2001) found only weak effects of interspecific competition between *M. ochrogaster* and *M. pennsylvanicus* in field experiments. When considering the same two species, Klatt (1986) concluded from field trials that advantage accrued to the species first occupying a site. Tazik and Getz (2007) observed interspecific territorial behavior between *M. Ochrogaster* and *M. pennsylvanicus* at low to moderate population densities in bluegrass. Finally, Haken and Batzli (1996) found that the diet of *M. ochrogaster* changed in the presence of *M. pennsylvanicus*, but only under conditions of low availability of high quality food and high densities of voles. Batzli et al. (1999) provided evidence that *M. pennsylvanicus* reduced densities of *M. ochrogaster*, whereas, Krebs (1977) found only minor negative

interactive effects of coexisting populations of the two species. Most of the above studies were either short-term experimental studies or involved only one habitat.

As a part of a 25 year study of population dynamics of *M. ochrogaster* and *M. pennsylvanicus* (Getz et al., 1987, 2001), we conducted 10 – 20 year manipulative studies in open populations to test the role of interspecific competition in the dynamics of these two coexisting species of voles. Experimental manipulations involved removal of one species from marginal (bluegrass) and low (tallgrass) quality food habitats to reduce interspecific competition. Specifically, we tested the hypotheses that there are negative interspecific interactions between coexisting populations of *M. ochrogaster* and *M. pennsylvanicus* that result in depressed densities of the other species and asynchronous population fluctuations. Because of time and space constraints, we were unable to replicate our study sites. Rather, we opted for larger study sites to reduce local site condition bias and for long-term manipulations, to reduce short-term temporal bias.

## 1 Methods and materials

### 1.1 Study sites

The study sites were located in the University of Illinois Biological Research Area (“Phillips Tract”), 6 km NE of Urbana, Illinois, USA (40°15'N, 88°28'W). Populations of *M. ochrogaster* and *M. pennsylvanicus* were monitored monthly in two habitats: bluegrass *Poa pratensis* and restored tallgrass prairie (a mixture of big bluestem, *Andropogon gerardii*; Indian grass, *Sorghastrum nutans*; and switch grass, *Panicum* spp.). Tallgrass prairie was the original habitat of both species in Illinois, whereas bluegrass, an introduced species, represents one of the more common habitats in which the two species can be found today in Illinois. Tallgrass is a very low food habitat, whereas bluegrass provides an intermediate food source (Cole and Batzli, 1979; Lindroth and Batzli, 1984; Thompson, 1965).

The restored tallgrass prairie was established in 1968. When the sites were first trapped in September 1977, prairie vegetation was well established. Lindroth and Batzli (1984) recorded relative abundances of the most prominent plant species: *Andropogon gerardii* (38%); Chinese lespedeza *Lepedeza cuneata* (25%); Beard tongue foxglove *Penstemon digitalis* (16%); and *Sorghastrum nutans* (19%). All other species represented < 1% relative abundance.

Bluegrass study sites were established within a former bluegrass pasture that was released from grazing in spring 1971. Relative abundances of plants in the sites were: *P. pratensis* (70%); dandelion, *Taraxacum officinale* (14%); wild parsnip, *Pastinaca sativa* (4%); goat's beard, *Tragopogon pratensis* (3%); about 20 other species with relative abundance of  $\leq 1\%$  (Getz et al., 1979).

### 1.2 Field methods

All study sites were organized on a 10 m interval grid system. 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 08:00 h and 15:00 h on the following three days. All animals were toe-clipped at first capture for individual identification ( $\leq 2$  toes/foot). All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet the guidelines recommended by the American Society of Mammalogists (Animal Care Committee, 1998).

Species, grid station, individual identification, sex, reproductive condition (males, testes abdominal or scrotal; females, vagina open or closed, pregnant as determined by palpation, or lactating), and body mass to the nearest 1 g were recorded at each capture. Animals were grouped by age based on body mass: adult,  $\geq 30$  g; juvenile,  $\leq 29$  g (Hasler, 1975).

### 1.3 Manipulations

The manipulations were carried out in a 2 ha (80 × 250 m) bluegrass site (Getz et al., 2001) surrounded on the north, west, and south sides by cultivated fields or unsuitable vole habitat and on the east by a 2 ha alfalfa field (south 130 m) and an 0.8 ha bluegrass site (north 120 m). Aluminum flashing buried 0.5 m below the surface and extending 0.5 m above the surface divided the bluegrass field into two, 1 ha sites.

All *M. ochrogaster* were removed from the south 1 ha bluegrass site (*M. pennsylvanicus* alone) from March 1977 through June 1987. *M. pennsylvanicus* were removed from the north 1 ha bluegrass site (*M. ochrogaster* alone) from March 1977 through May 1997. The adjacent 0.8 ha bluegrass site served as the control for the *M. pennsylvanicus* alone and the *M. ochrogaster* alone sites from 1977 – 1987; both species were allowed to inhabit the south 1 ha bluegrass site from 1987 – 1997, thus serving as the control for the *M. ochrogaster* alone site during these years.

Trapping in the 0.8 ha control sited from 1974 – 1976 by Cole and Batzli (1978) suggested this site provided suitable habitat for *M. ochrogaster*; they removed immigrant *M. pennsylvanicus* during their study. Both species were allowed to remain in the north 1 ha site from October 1971 – June 1977 and in the south 1 ha site from July 1987 – May 1997. Demographic data for these periods (Getz et al., 2001, 2005b) indicated both sites afforded suitable habitat for both species.

A 2.6 ha (72 × 360 m) site in Phillips tract (Getz

et al., 2001) was used for the tallgrass manipulative study. The site was surrounded on three sides by cultivated fields and on the east (72 m) side by a site that underwent succession from a forb stage to shrubs and trees during the course of the study.

Because *M. ochrogaster* populations were very low and *M. pennsylvanicus* very high in tallgrass for most of the study period (Getz et al., 2001), only effects of *M. pennsylvanicus* on *M. ochrogaster* were tested in tallgrass. We removed *M. pennsylvanicus* from a 0.5 ha (72 × 75 m) tallgrass site at the west end of the tallgrass prairie from September 1984 through May 1997; a 0.5 ha site at the east end of the prairie served as the control. From July 1977 through April 1984 both species were allowed to remain in the west 0.5 ha site. Population densities of *M. pennsylvanicus* during this time indicated the site was suitable for the species.

Removed animals were released on the opposite side of an Interstate highway, approximately 1 km from the study sites. None returned to the study sites.

#### 1.4 Data analysis

We estimated survival as the proportion of animals (total population) that survived from one month to the next. Animals that weighed  $\leq 29$  g when first captured were presumed to have been born on the study site since the last monthly trapping session. We calculated persistence of these animals as the time elapsed from first capture to their disappearance from the site; young voles captured in only one month were given a persistence of one month. 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 monthly trapping session (Dueser et al., 1981; Getz et al., 2005a; Tamarin, 1984). We calculated the number of immigrants per month, adjusted to number of immigrants/ha. We also calculated for each month the proportion of adult females that had been recorded as reproductively active (vagina open, pregnant, or lactating). We compared population density, survival, persistence of young, proportion of immigrants, proportion of reproductively active adult females, and in the site where each species was alone (“experimental”) with the site where both species were present (“control”).

We analyzed our data within the capture-mark-recapture (CMR) framework (Lebreton et al., 1992; Williams et al., 2001). We implemented CMR methods using Program MARK (White and Burnham, 1999) to estimate demographic parameters, to test specific hypotheses regarding these parameters, and to evaluate the effect of removal of the competitor species. Specifically, we used Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965) to estimate apparent survival ( $\phi$ ) and recapture rates ( $\rho$ ), and to test for variation in survival rates among experimental groups and through time. Because the CMR model did not

provide useable estimates of population density and survival at very low densities, we excluded extended trough periods (periods with  $< 20$  voles per ha) from our analysis.

We applied goodness-of-fit tests using RELEASE TEST 2 + 3 (in program MARK) to test if our global model fits the data. When the dispersion parameter ( $\hat{c}$ ) was greater than 1, we corrected for over-dispersion using the calculated  $\hat{c}$ . Next, we used Akaike’s information criterion corrected for small sample size and adjusted for quasi-likelihood (QAIC<sub>c</sub>) for model comparison, and for the identification of the most parsimonious model; the lower the QAIC<sub>c</sub> value, the more parsimonious the model. The most parsimonious model in the candidate model set was compared to neighboring models based on the differences in QAIC<sub>c</sub> values,  $\Delta\text{QAIC}_c$ . If  $\Delta\text{QAIC}_c < 2$ , both models are equally supported by the data. If  $2 < \Delta\text{QAIC}_c < 7$ , there is considerable support for a real difference between the models, and if  $> 7$ , there is a strong evidence for a difference between the models (Burnham and Anderson, 2002).

We performed our analyses separately for three species-habitat combinations: (1) *M. ochrogaster* in bluegrass habitat, (2) *M. ochrogaster* in tallgrass, (3) *M. pennsylvanicus* in bluegrass habitat (Table 1). Because study duration was up to 20 years in some sites and included extended trough periods, it was not possible to run a single model for each species-habitat combination. We, therefore, divided the data into shorter periods, which resulted in two data sets for *M. ochrogaster* in bluegrass habitat (data sets # 1 and # 2), two data sets for *M. ochrogaster* in tallgrass habitat (data sets # 3 and # 4), and one data set for *M. pennsylvanicus* in bluegrass habitat (data set # 5; Table 1). Our preliminary analysis showed that survival rates did not differ significantly between sexes in either species; therefore, for each species, we combined data for both sexes in all further analyses.

Effects of competitor removal on survival and recapture rates were analyzed by examining both combined and additive effects of competitor removal and time (Williams et al., 2001). For example, a model denoted as (exp\* time) includes main effects of competitor removal and time, and also the interaction effect between these two covariates, whereas (exp + time) includes only the main effects of competitor removal and time. The time effect was included as a fixed effect (i. e., separate estimates for each month).

We also tested for correlations between population density of one species and monthly survival rates, and proportion of reproductively active females of the other species in the bluegrass control site from March 1977 – June 1987. These analyses tested potential effects of the coexisting species on each other within a site and were limited to the time the site served as a control for the

experimental sites. In order to reduce autocorrelation effects, we used data from every other month for these analyses. The CMR model did not provide useable estimates of population density and survival at densities < 20 voles/ha, which was greater than the mean density of the two species in bluegrass (Getz et al., 2001); we, therefore, utilized data from Getz et al. (2001) for these analysis. Because interspecific effects may be most pronounced during periods of low resources, e. g., low

food availability during winter, we also tested for correlations between population density of a species and survival and proportion reproductively active females of the other species during December – February.

All original capture data and explanatory files from the 25-year study are available to anyone wishing to make use of them at: <http://www.life.uiuc.edu/getz/> and <http://hdl.handle.net/2142/172>.

**Table 1** Description of each dataset used for capture-mark-recapture analysis: species, habitat, start and end dates, study duration and number of voles in control and experimental groups that were used in CMR analysis for each species-habitat combination

Dataset	Species	Habitat	Start month	End month	Duration	Number of voles*	
						Control	Experiment
# 1	<i>M. ochrogaster</i>	Bluegrass	November 1982	June 1987	56 months	776	684
# 2	<i>M. ochrogaster</i>	Bluegrass	July 1987	March 1991	45 months	524	599
# 3	<i>M. ochrogaster</i>	Tallgrass	October 1984	April 1987	31 months	435	292
# 4	<i>M. ochrogaster</i>	Tallgrass	August 1987	February 1991	43 months	479	200
# 5	<i>M. pennsylvanicus</i>	Bluegrass	May 1977	September 1982	65 months	547	842

\* Excluding the number of competitor species.

## 1.5 Statistical analyses

We used paired-sample t-tests to compare within each habitat persistence of young, proportion of reproductively active adult females, and number of immigrants between experimental and control sites. 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. For variables that were “zero” we added 0.001 prior to transformation. SPSS 10.0.7 for Macintosh (SPSS, Inc., 2001) was used for these statistical analyses.

## 2 Results

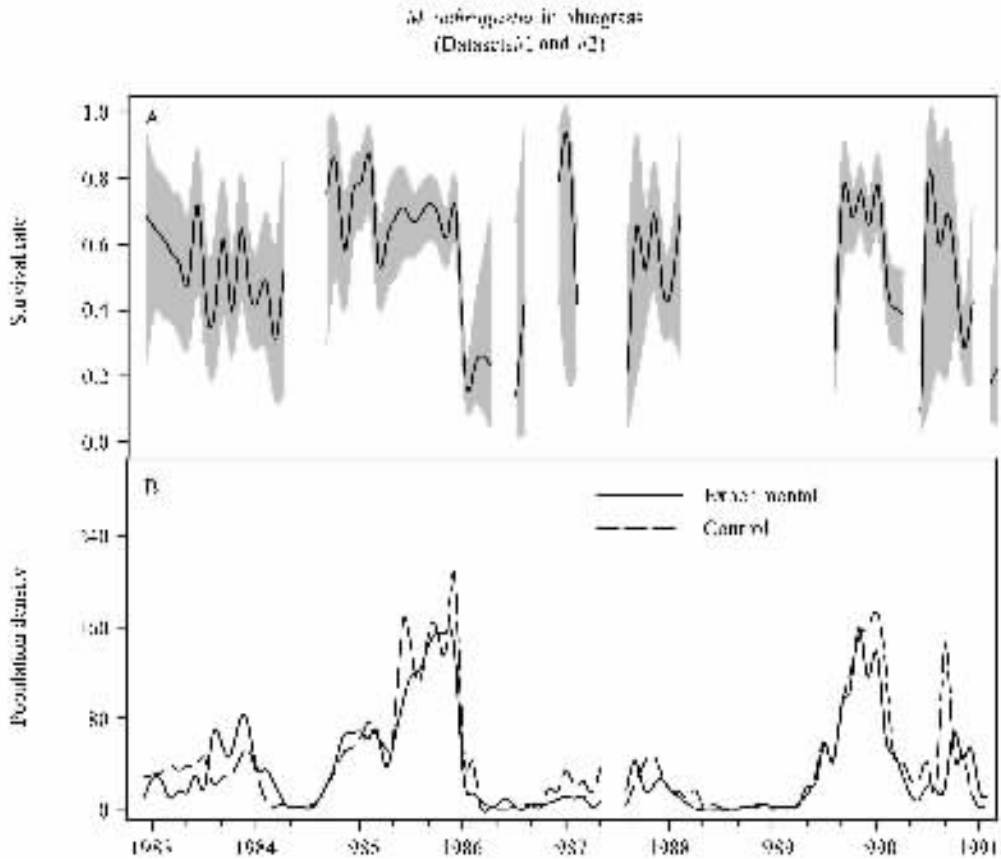
### 2.1 Population density

In bluegrass, mean population density of *M. ochrogaster* was lower in the experimental than in the control site (Mean  $\pm$  SE,  $35.5 \pm 4.2$  and  $41.1 \pm 4.9$  voles/ha, respectively;  $t = 2.381$ ,  $df = 96$ ,  $P = 0.019$ ; Fig.1). In tallgrass, amplitudes of fluctuation of *M. ochrogaster* and mean population density were higher in the experimental than control site (Mean density,  $76.6 \pm 9.2$  and  $37.7 \pm 6.2$  voles/ha, respectively;  $t = 8.002$ ,  $df = 69$ ,  $P < 0.001$ ; Fig.2). Mean population density of *M. pennsylvanicus* in bluegrass was lower in the experimental than in the control site ( $30.6 \pm 3.4$  and  $55.0 \pm 4.6$  voles/ha, respectively;  $t = 6.170$ ,  $df = 62$ ,  $P < 0.001$ ; Table 3). Because *M. pennsylvanicus* densities were high in tallgrass at all times (Getz et al., 2001), it appeared that there was no suppressing effect of *M. ochrogaster* on *M. pennsylvanicus* in this habitat.

### 2.2 Demographic variables

Goodness-of-fit tests indicated that the global CJS model fit the data with a moderate under-dispersion ( $< 1.0$ ) in one data set (*M. pennsylvanicus* in bluegrass; Table 2). In the other four data sets, there were slight over-dispersions ( $1.0 < \hat{c} < 3.0$ ), and we used the calculated  $\hat{c}$  values for quasi-likelihood adjustment of models and their parameter estimates (Table 3). Our analyses using CJS models showed that the most parsimonious recapture rate models differed among the five data sets (Table 1). It included no effect in data sets # 1 and # 4 (Models # 2 and # 17, Table 3), additive effects of competitor removal and time in data set # 2 (Model # 8), only a time effect in data set # 3 (Model # 12), and interactive effects of competitor removal and time in data set # 5 (Model # 21).

The most parsimonious survival rate model included only the time effect in data sets # 1, # 2 and # 5, the effect of competitor removal in data set # 3, and the additive effects of competitor removal and time in data set # 4 (Table 3). Survival rates varied substantially through time in data sets # 1, # 2, # 4, and # 5, but not in dataset # 3 (Figures 1 – 3). The effect of competitor removal was included in the most parsimonious models for data sets # 3 and # 4 (*M. ochrogaster* in tallgrass). Comparison of the average survival rates in the experimental and control groups indicated that competitor removal might have had a slight positive effect on *M. ochrogaster* in tallgrass habitat (Fig.4). However,  $\Delta QAIC_c$  between these models and those that excluded the effect of competitor removal was less than 2, indicating that this effect was not substantial.



**Fig.1** Temporal variation in monthly survival rates of *M. ochrogaster* in bluegrass habitat (A) and monthly estimates of population densities (individuals/hectare) are given for competitor removal and control sites (B)

Because competitor removal did not significantly influence survival, survival rates were estimated using model  $\{\phi(\text{month}) \rho(\cdot)\}$  for data set #1 and model  $\{\phi(\text{month}) \rho(\text{exp} + \text{month})\}$  for data set #2 (Table 3). Grey shaded area indicates 95% confidence intervals.

**Table 2** Goodness-of-fit tests for the global Cormack-Jolly-Seber models for each dataset

Dataset	Species: habitat	Model deviance	Degrees of freedom	P-level	$\hat{c}$ correction
# 1	<i>M. ochrogaster</i> : bluegrass	259.2	189	>0.001	1.37
# 2	<i>M. ochrogaster</i> : bluegrass	138.7	112	0.045	1.24
# 3	<i>M. ochrogaster</i> : tallgrass	199.2	83	>0.001	2.40
# 4	<i>M. ochrogaster</i> : tallgrass	167.5	119	>0.001	1.41
# 5	<i>M. pennsylvanicus</i> : bluegrass	196.6	270	0.999	0.73

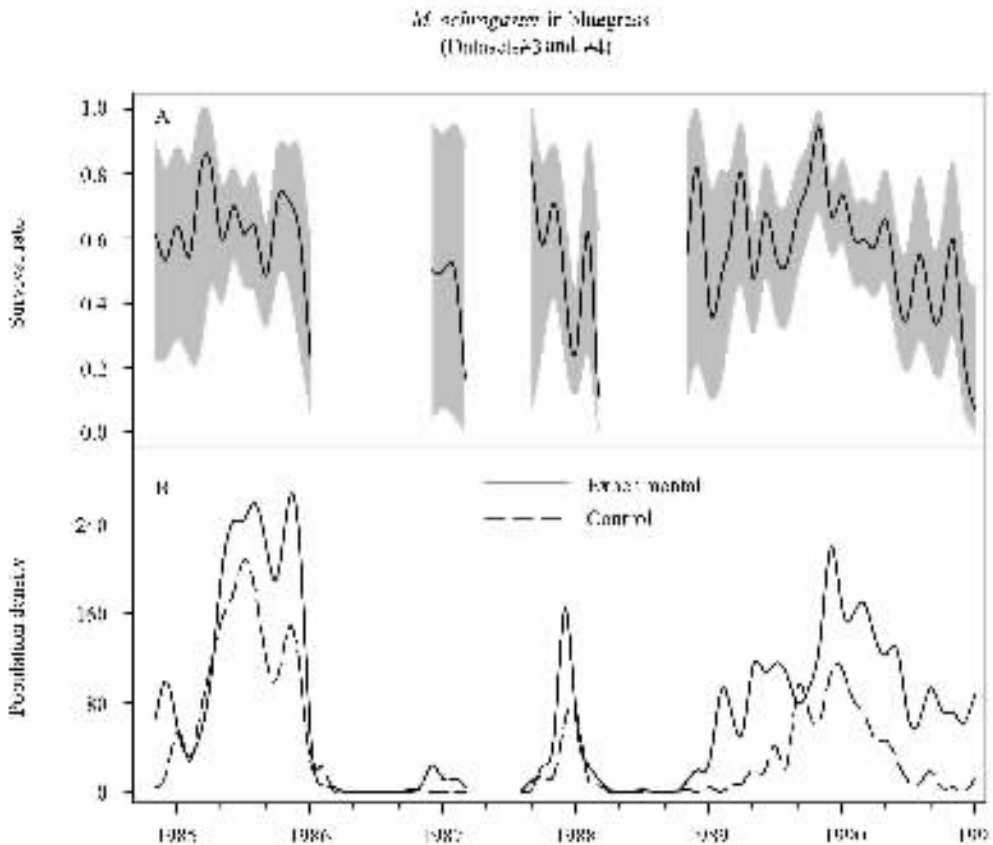
The values of the variance inflation factor ( $\hat{c}$ ) also are given.

For *M. ochrogaster* in bluegrass, persistence of young did not differ between the experimental and control sites ( $1.9 \pm 0.1$  and  $2.0 \pm 0.1$  months, respectively;  $t = 0.672$ ,  $df = 312$ ,  $P = 0.502$ ). The proportion of reproductively active females ( $0.65 \pm 0.03$  and  $0.76 \pm 0.03$ , respectively;  $t = 2.102$ ,  $df = 99$ ,  $P = 0.038$ ) was lesser in the experimental than the control site. The number of immigrants was lower in the experimental than the control site ( $3.0 \pm 0.4$  and  $3.6 \pm 0.4$  immigrants/ha, respectively;  $t = 3.471$ ,  $df = 239$ ,  $P = 0.001$ ).

For *M. ochrogaster* in tallgrass, persistence of young

( $2.3 \pm 0.1$  and  $2.2 \pm 0.1$  months, respectively;  $t = 0.247$ ,  $df = 61$ ,  $P = 0.806$ ) and proportion of reproductively active females ( $0.64 \pm 0.07$  and  $0.66 \pm 0.05$ , respectively;  $t = 0.957$ ,  $df = 22$ ,  $P = 0.349$ ) did not differ between the experimental and control sites. The number of immigrants was greater in the experimental than in the control site ( $2.6 \pm 0.4$  and  $2.0 \pm 0.4$  immigrants/ha, respectively;  $t = 4.475$ ,  $df = 147$ ,  $P < 0.001$ ).

For *M. pennsylvanicus* in bluegrass, persistence of young did not differ between experimental and control



**Fig.2** Temporal variation in monthly survival rates of *M. ochrogaster* in tallgrass habitat (A) and monthly estimates of population densities (individuals/hectare) are given for competitor removal and control sites (B)

Because competitor removal did not significantly influence survival, survival rates were estimated using model  $\{\phi(\text{month}) \rho(\text{month})\}$  for data set #3 and model  $\{\phi(\text{month}) \rho(\cdot)\}$  for data set #4 (Table 3). Grey shaded area indicates 95% confidence intervals.

sites ( $2.2 \pm 0.1$  and  $2.1 \pm 0.1$  months, respectively;  $t = 0.425$ ,  $df = 275$ ,  $P = 0.671$ ). Proportion of reproductively active females did not differ between the experimental and control sites ( $0.56 \pm 0.04$  and  $0.60 \pm 0.04$ , respectively;  $t = 1.422$ ,  $df = 74$ ,  $P = 0.159$ ), and immigrants were slightly fewer in the experimental than control site ( $2.8 \pm 0.3$  and  $3.8 \pm 0.6$  immigrants/ha, respectively;  $t = 2.154$ ,  $df = 119$ ,  $P = 0.033$ ).

### 2.3 Correlation analyses

Population densities of *M. ochrogaster* and *M. pennsylvanicus* were negatively correlated in the bluegrass control site ( $r = -0.417$ ,  $n = 62$ ,  $P = 0.001$ ). Monthly survival of *M. ochrogaster* and *M. pennsylvanicus* in bluegrass was not correlated, whether for all months ( $r = 0.157$ ,  $n = 36$ ,  $P = 0.361$ ) or only winter months ( $r = 0.143$ ,  $n = 17$ ,  $P = 0.584$ ). Proportion of reproductively active females of the two species was correlated for all months ( $r = 0.635$ ,  $n = 34$ ,  $P < 0.001$ ), but not for the winter months alone ( $r = 0.434$ ,  $n = 15$ ,  $P = 0.160$ ).

Monthly survival of *M. pennsylvanicus* in bluegrass was not correlated with population density of

*M. ochrogaster*, whether for all months ( $r = 0.021$ ,  $n = 49$ ,  $P = 0.885$ ) or for winter alone ( $r = 0.055$ ,  $n = 23$ ,  $P = 0.803$ ), or for lag periods of up to three months. Neither was the proportion of reproductively active female *M. pennsylvanicus* correlated with population density of *M. ochrogaster* (all months:  $r = 0.033$ ,  $n = 49$ ,  $P = 0.824$ ; winter:  $r = 0.012$ ,  $n = 23$ ,  $P = 0.958$ ). The proportion of reproductively active female *M. pennsylvanicus* was positively correlated with population density of *M. ochrogaster* at a lag period of three months, but not for one or two month lags. Monthly survival of *M. ochrogaster* in bluegrass was negatively correlated with population density of *M. pennsylvanicus* for all months ( $r = 0.422$ ,  $n = 49$ ,  $P = 0.003$ ), including lag periods of one to three months, but not for winter alone ( $r = 0.322$ ,  $n = 24$ ,  $P = 0.124$ ). The proportion of reproductively active female *M. ochrogaster* was not correlated with population density of *M. pennsylvanicus* (all months:  $r = 0.023$ ,  $n = 40$ ,  $P = 0.890$ ; winter:  $r = 0.037$ ,  $n = 23$ ,  $P = 0.867$ ), including lag periods of one to three months.

**Table 3 Analysis of the effect of competitor removal on vole survival and recapture rates**

No.	Model	$\Delta\text{QAIC}_c$	QAIC <sub>c</sub> Weight	Number of parameters	Deviance
Dataset # 1: <i>M. ochrogaster</i> in bluegrass habitat					
1	$\phi$ (month) $\rho$ (month)	0.00	0.31	84	998.8
2	$\phi$ (month) $\rho$ (.)	0.75	0.21	47	1 077.1
3	$\phi$ (exp + month) $\rho$ (month)	1.71	0.13	85	998.4
4	$\phi$ (exp + month) $\rho$ (.)	2.31	0.10	48	1 076.6
5	$\phi$ (month) $\rho$ (exp)	2.82	0.08	48	1 077.1
Dataset # 2: <i>M. ochrogaster</i> in bluegrass habitat					
6	$\phi$ (month) $\rho$ (exp * month)	0.00	0.42	75	567.3
7	$\phi$ (exp + month) $\rho$ (exp * month)	0.54	0.32	77	563.5
8	$\phi$ (month) $\rho$ (exp + month)	1.30	0.22	58	604.9
9	$\phi$ (exp + month) $\rho$ (exp + month)	6.51	0.02	61	603.8
10	$\phi$ (exp + month) $\rho$ (month)	8.15	0.01	59	609.7
Dataset # 3: <i>M. ochrogaster</i> in tallgrass habitat					
11	$\phi$ (exp) $\rho$ (month)	0.00	0.31	22	338.8
12	$\phi$ (.) $\rho$ (month)	1.13	0.18	21	342.0
13	$\phi$ (.) $\rho$ (exp + month)	1.19	0.17	22	340.0
14	$\phi$ (exp) $\rho$ (exp + month)	1.39	0.16	23	338.1
15	$\phi$ (exp + month) $\rho$ (.)	3.04	0.07	23	339.8
Dataset # 4: <i>M. ochrogaster</i> in tallgrass habitat					
16	$\phi$ (exp + month) $\rho$ (exp)	0.00	0.33	37	651.4
17	$\phi$ (exp + month) $\rho$ (.)	0.91	0.21	36	654.5
18	$\phi$ (month) $\rho$ (exp + month)	1.56	0.15	60	603.7
19	$\phi$ (month) $\rho$ (exp)	4.70	0.03	36	658.3
20	$\phi$ (month) $\rho$ (.)	9.23	0.00	35	664.9
Dataset # 5: <i>M. pennsylvanicus</i> in bluegrass habitat					
21	$\phi$ (month) $\rho$ (exp * month)	0.00	0.69	166	1 703.6
22	$\phi$ (exp * month) $\rho$ (exp * month)	2.07	0.25	201	1 624.5
23	$\phi$ (exp + month) $\rho$ (exp * month)	4.86	0.06	169	1 701.6
24	$\phi$ (exp) $\rho$ (exp * month)	15.67	0.00	118	1 826.8
25	$\phi$ (.) $\rho$ (exp * month)	17.41	0.00	118	1 828.5

Differences in Akaike's Information Criterion corrected for small sample size and adjusted for quasi-likelihood ( $\Delta\text{QAIC}_c$ ), QAIC<sub>c</sub> weights, number of parameters and model deviances are given for each model. Symbols are:  $\phi$  = apparent survival rate,  $\rho$  = recapture rate, exp = effect of competitor removal, and month = time effect. A plus sign (+) denotes additive effects, and a multiplication sign (\*) denotes interaction effect. A period (.) indicates constant value of the parameter (model with intercept only). Only five most parsimonious models are given for each dataset. The most parsimonious model for each dataset is indicated in bold.

### 3 Discussion

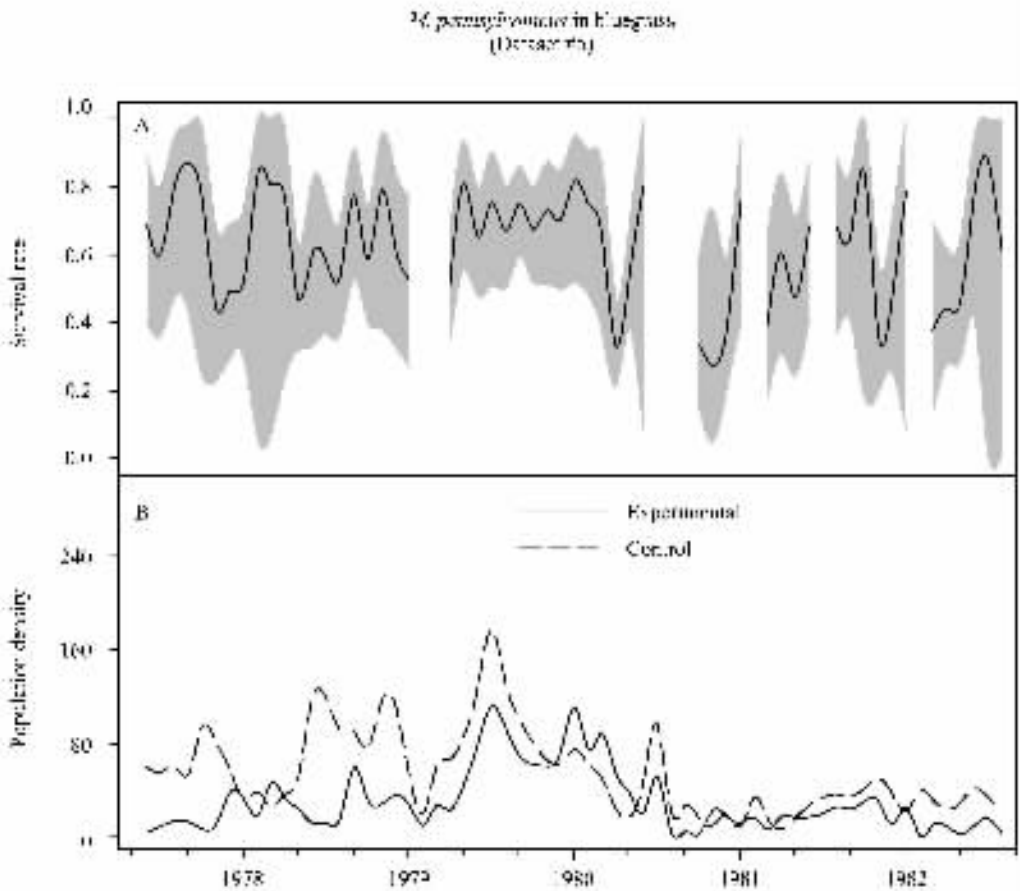
Results of experimental removal of *Microtus ochrogaster* and *M. pennsylvanicus* from open populations in bluegrass and tallgrass habitats, indicated demography of coexisting populations of the two species was not negatively affected by interspecific interactions where food resources were at least moderately high (bluegrass). In fact, population densities of both species in bluegrass were higher where the two species coexisted, e. g., the control site. Only demography of *M. ochrogaster* was negatively affected by presence of *M. pennsylvanicus* in low food resource tallgrass. Krebs (1977) also found no suppressive interaction between these two species where food resources were adequate.

For *M. ochrogaster* in bluegrass, population

densities, proportion reproductively active females, and number of immigrants were greater in a site where the two species coexisted than where alone. Monthly survival and persistence of young on the site did not differ between the experimental and control sites. Population densities of *M. pennsylvanicus* in bluegrass sites also were higher where the two species coexisted than where alone. Further, survival, persistence of young, proportion reproductively active females, and number of immigrants did not differ between experimental and control sites.

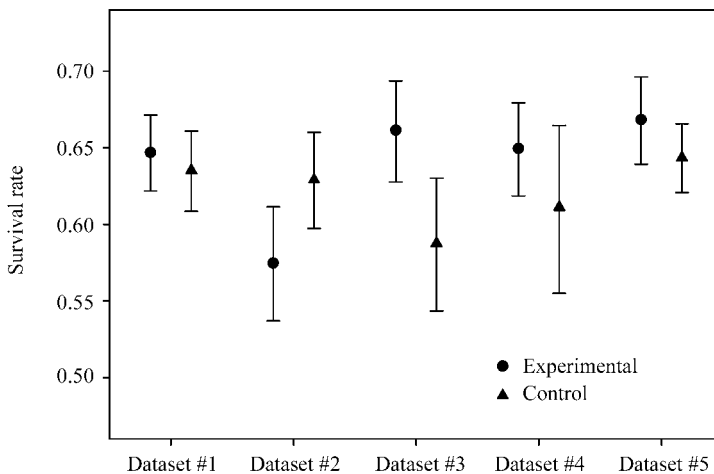
*Microtus pennsylvanicus* exerted a strong suppressing effect on population densities of *M. ochrogaster* in tallgrass. Survival, persistence of young, and proportion reproductively active females did not differ, however, between sites where *M. ochrogaster* was alone and where *M. pennsylvanicus* were present. Only the number of





**Fig.3** Temporal variation in monthly survival rates of *M. pennsylvanicus* in bluegrass habitat (A) and monthly estimates of population densities (individuals/hectare) are given for competitor removal and control sites (B)

Because competitor removal did not significantly influence survival, survival rates were estimated using model  $\{\phi(\text{month}) \rho(\text{exp} * \text{month})\}$  for data set # 5 (Table 3). Grey shaded area indicates 95 % confidence intervals.



**Fig.4** Average monthly survival rate estimates for experimental and control groups in each of the five datasets

Mean values and 95% confidence intervals were estimated using the models that included only the removal effect on survival rate  $\{\phi(\text{exp})\}$ . See Table 1 for the description of each dataset.

immigrants was slightly greater where *M. ochrogaster* was alone, insufficiently so to affect population densities. Monthly survival of *M. ochrogaster* may have been slightly

higher in the experimental than the control site, but the affect on population density would have been inconsequential. Presence of *M. ochrogaster* did not

appear to affect demography of *M. pennsylvanicus* in tallgrass (Getz et al., 2001).

Effects of season, especially periods of low food availability, as occur in winter, could not be tested with the CMR model; data for the trough phase were too few for detailed analyses of survival. Sample sizes also were too small to test for seasonal differences in the other variables between the experimental and control sites. Correlation analyses of effects of density of one species on the other for coexisting populations in bluegrass indicated, however, no effect of population density on any demographic variable during winter. In the bluegrass control site, survival and the proportion of reproductively active female *M. pennsylvanicus* were not correlated with population density of *M. ochrogaster*, whether all seasons or only winter were included in the analyses. Survival, but not proportion reproductively active female *M. ochrogaster*, was negatively correlated with population densities of *M. pennsylvanicus* when all seasons were included in the analyses. Survival of *M. ochrogaster* during winter, however, was not correlated with population density of *M. pennsylvanicus*.

The proportion of reproductively active female *M. pennsylvanicus* and *M. ochrogaster* were positively correlated in bluegrass, suggesting that what was good for reproduction of *M. pennsylvanicus* was also good for reproduction of *M. ochrogaster*. In contrast, survival of the two species was not correlated, indicating that the species were subjected to different mortality factors (Getz et al., 2005b). Differential mortality, not reproduction, thus appears to be the primary factor responsible for the negative correlation in population densities of the coexisting species within a site.

Of 25 population fluctuations of *M. ochrogaster* and 14 of *M. pennsylvanicus* during the 25 years of the general study, there were only two instances of synchrony of population fluctuations of the two species, both in bluegrass (Getz et al., 2001). Klatt (1986) studied *M. ochrogaster* and *M. pennsylvanicus* populations at the same study sites and concluded competitive advantage to the species first entering a site. Tazik and Getz (2007) provided evidence for interspecific territorial behavior between females of the two species, at low to moderate population densities. Getz et al. (2005a) have shown that the number of immigrants of *M. ochrogaster* and *M. pennsylvanicus* into a site is very low most months, thus creating conditions for competitive exclusion of a species through interspecific territorial behavior. We suggest that at very low densities, interspecific territorial behavior allowed sufficient resources for survival and reproduction of the two species. The species with the greatest number of immigrants into a site may have suppressed population growth of the other species through direct effects of interspecific territorial behavior. Thus, over the long term, there would have been reduced

opportunity for sufficient interspecific interactions to negatively affect demographic variables of the coexisting species. As we observed in our studies, the two species seldom occurred sympatrically at high densities.

Getz et al. (2006 a, b) suggested that population densities of *M. ochrogaster* and *M. pennsylvanicus* in our study sites were kept at low densities much of the time by the net effect of predation from multiple generalist predators. Population densities of generalist predator species most likely were controlled by factors in addition to vole densities within our study sites. Because of the independent nature of population fluctuations of such diverse predator species as raptors, large and small mammals, and snakes, as well as variation in numerical and functional responses of these predators (Pearson, 1985), we speculate the net effects of predation may be greater in some years than in others. During years with high predation effects, one or both species may have disappeared from the site. At these times, the species remaining at low densities in the site, or the first one to recolonize the site, may have impeded settlement of immigrants of the other species through interspecific territorial behavior. In this manner, interspecific interactions may have been involved in non synchronous population fluctuations of *M. ochrogaster* and *M. pennsylvanicus* within a site. When populations of both species eventually achieved high densities in a site, however, there was no evidence for interspecific interference in the demography of either species where food resources were relatively high (bluegrass). Where food resources (tallgrass) were limited, presence of *M. pennsylvanicus* appeared to suppress population density of *M. ochrogaster*. The only variable significantly reduced, however, was immigration, not a primary factor involved in population demography of this species (Getz et al., 2005a). Lin and Batzli (2001) also less immigration of *M. ochrogaster* into sites with dense cover when *M. pennsylvanicus* was present.

Our results agreed in general with those of Huitu et al. (2004), Eccard and Ylönen (2002, 2003a, b), and Johannesen (2003) that interspecific interactions between coexisting species of arvicoline rodents are seldom sufficient to negatively affect population demography of the species. Huitu et al. (2004) suggested predation effects may keep densities of coexisting competing species sufficiently low that there is no negative interaction effect. Eccard and Ylönen (2002) concluded that direct interference, as in territorial defense, may negatively affect demography and result in little indirect negative interference, i. e., on survival and reproduction. That there seldom were concurrent population fluctuations of *M. ochrogaster* and *M. pennsylvanicus*, although they coexisted in the same habitats, may reflect similar responses. Typically, populations of the two species did not coexist in sufficient numbers to elicit interspecific

demographic effects.

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