

Effects of conspecific and heterospecific residents on patterns of immigration in two species of voles

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Studies with birds have shown that presence and density of resident conspecifics and heterospecifics can influence patterns of habitat selection. There have been few studies on the effects of social cues on rates of immigration in mammals. We report results from a long-term live trapping study of immigration in two species of voles, *Microtus ochrogaster* Wagner, 1842 and *Microtus pennsylvanicus* Ord, 1815, in bluegrass habitat in east-central Illinois, USA. We compare immigration into control sites from which no individuals of either species were removed with immigration into experimental sites from which either conspecifics or heterospecifics were removed. We focus on characteristics of immigrants and rates of immigration in relation to density in destination habitats. Within each species, immigrants into control and removal sites were similar with respect to body mass and reproductive condition, indicating no major differences in the physical condition of immigrants into sites with established populations and sites without established populations. For both species, density of conspecifics at a site positively influenced rate of immigration at that site. Density of heterospecifics at destination sites did not significantly influence rate of immigration for either species. These results suggest that site selection by dispersing *M. ochrogaster* and *M. pennsylvanicus* is characterized by conspecific attraction.

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Introduction

During habitat selection, individuals may base search and settlement decisions on several factors, including aspects of the physical environ-

ment, such as food availability and type and structure of vegetation. Sometimes, however, characteristics of the physical environment are difficult or impossible to assess in a timely manner, and social cues from individuals with similar ecological needs may be used as indicators of habi-

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tat quality (Stamps 2001). For example, presence of conspecifics or heterospecifics has been shown to positively influence patterns of settlement after dispersal or migration in some species of birds, either at all densities or at low to moderate densities (eg, Thomson *et al.* 2003, Fletcher 2007). Such findings contrast with traditional views that individuals searching for a place to settle should typically avoid conspecifics and heterospecifics, and thereby avoid antagonistic encounters and competition for resources. Other species of birds appear to avoid areas with heterospecifics during habitat selection (eg, Fletcher 2007).

Relatively few studies have examined how resident densities influence settlement in mammals. For translocated black rhinos *Diceros bicornis*, the density of conspecifics in destination reserves was the best predictor of mortality risk, with increased risk associated with higher densities of conspecifics (Linklater and Swaisgood 2008). In voles, some studies have found dispersers avoid conspecifics (eg, Dueser *et al.* 1981, Danielson and Gaines 1987), whereas others have observed dispersers to be attracted to conspecifics (eg, Meserve and Klatt 1985, Diffendorfer *et al.* 1995, Getz *et al.* 2005). In addition to influencing rate of immigration, presence of conspecifics has been suggested to influence the characteristics of immigrants. Danielson *et al.* (1986) predicted that immigrants into established populations might be relatively larger, given the presumed difficulty of settling in a population of unfamiliar and potentially hostile residents. There is, however, no evidence for whether immigrants into a habitat occupied by conspecifics differ physically from immigrants into an unoccupied habitat of the same quality.

Presence of heterospecifics can also influence habitat selection in voles. Danielson and Gaines (1987), using field enclosures, found that presence of *Synaptomys cooperi* inhibited colonization by *Microtus ochrogaster* Wagner, 1842, but presence of *Sigmodon hispidus* did not, even though both species were competitors of *M. ochrogaster*. Lin and Batzli (2001a) simultaneously released individuals of *M. ochrogaster* and *M. pennsylvanicus* Ord, 1815 into field enclosures with habitat patches differing in vegetative cover and food

quality. *Microtus ochrogaster* and *M. pennsylvanicus* coexist in several habitats in mid-western North America and exhibit similar preferences with respect to diet (Lindroth and Batzli 1984, Haken and Batzli 1996) and habitat (Klatt and Getz 1987). Nevertheless, Lin and Batzli (2001a) found *M. pennsylvanicus* to have a limited, negative impact on habitat selection by *M. ochrogaster*, and reciprocal effects of *M. ochrogaster* on *M. pennsylvanicus* were not detected. Getz *et al.* (2005), studying open populations of *M. ochrogaster* and *M. pennsylvanicus*, found for both species that number of immigrants was positively correlated with population densities of the other species in tallgrass habitats. In alfalfa habitats, number of *M. pennsylvanicus* immigrants was negatively correlated with population densities of *M. ochrogaster*; the relationship in bluegrass was also negative, but failed to reach statistical significance.

In this paper we compare immigration of *M. ochrogaster* and *M. pennsylvanicus* into control sites from which no individuals of either species were removed with immigration into experimental sites from which either conspecifics or heterospecifics were removed. First we examine whether physical characteristics of immigrants (body mass and reproductive condition) differ between control and removal sites. Second, we examine whether the density of conspecifics or heterospecifics (on a site or in the general study area) influences the number of immigrants arriving at control or removal sites. All study areas were bluegrass habitat (a habitat of intermediate quality for both species) and all populations were open. These data were collected as part of a long-term field study of interactions between *M. ochrogaster* and *M. pennsylvanicus*, and depending on the particular comparison, represent either 10 or 20 years of continuous data. Getz *et al.* (2005) compared characteristics of residents and immigrants of the two species in three habitats (alfalfa, bluegrass, and tallgrass), and did not include data from removal sites. Based on results from unmanipulated bluegrass sites at our study area (Getz *et al.* 2005), we predicted that both species would be attracted to conspecifics, and would either avoid or be unaffected by heterospecifics.

Study area

All 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; Fig. 1 in Getz *et al.* 2005). We used three bluegrass sites from July 1977 through June 1987: (1) BGMo (a 1.0 ha site from which we removed all *M. pennsylvanicus* and left all *M. ochrogaster*); (2) BGMp (a 1.0 ha site from which we removed all *M. ochrogaster* and left all *M. pennsylvanicus*); and (3) BGCont (a 0.8 ha control site from which we did not remove individuals of either species). From July 1987 through May 1997, we continued to remove all *M. pennsylvanicus* from BGMo and to leave all *M. ochrogaster* there; thus, we have 20 years of data from that experimental site. Although removal of *M. ochrogaster* from the BGMp site ceased after June 1987, we continued live trapping at the site for another 10 years, not removing individuals of either species. We used data collected from BGMp from July 1987 through May 1997 as control data for BGMo. Thus, BGCont served as a control site for the first 10 years (1977–1987) and the BGMp site served as a control site for the next 10 years (1987–1997). Because of time constraints and limited availability of suitable study areas, we were unable to replicate our experiments. Nevertheless, the large size of the study sites and lengthy duration of the study should, at least in part, compensate for the lack of replication. Population densities and fluctuations of the non-removed species in the experimental sites were similar to those in the controls (Getz *et al.* 1987).

The study sites were established within a former bluegrass pasture released from grazing in spring 1971. Relative abundances of plants in the sites were as follows: bluegrass, *Poa pratensis* (70%); dandelion, *Taraxacum officinale* (14%); wild parsnip, *Pastinaca sativa* (4%); goat's beard, *Tragopogon pratensis* (3%; Getz *et al.* 1979). From 1977–1987 there was an aluminum flashing fence buried 0.5 m below the surface and extending 0.5 m above the surface between BGMo and BGCont and BGMp. Openings of ≈ 10 cm were located every 10 m along the fence. From 1984–1997 large enclosures were located in the area to the north of BGMo (Desy and Batzli, 1989). Other widely dispersed vole habitat within the area consisted of mown county roadsides (≈ 2 m wide), banks of drainage ditches (≈ 5 m wide), < 0.25 ha uncultivated sites, and margins (4–5 m wide) of an interstate highway 0.75 km from the study area. The study sites were mowed each year, in late summer, 25 cm above the surface to suppress growth of forbs and woody vegetation. The vegetation within the study sites remained relatively unchanged throughout the study (Getz *et al.* 2001).

Material and methods

Procedures

All study sites were organized on a 10 m interval grid system with 1 wooden multiple-capture live-trap (Burt 1940) 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 aluminium shields or vegetation to protect traps from the sun

during the summer. Wooden traps provided ample insulation in the winter, so we did not provide nesting material in the traps at any time. We estimated trap mortality to be < 0.5% and trappabilities to be 91% for *M. pennsylvanicus* and 92% for *M. ochrogaster* (Getz *et al.* 2001). Traps were set in the afternoon and checked at about 0800 h and 1500 h on the following three days. All voles that were released at the trap station were toe-clipped at first capture for individual identification (< 2 toes/foot). Some removed voles had been toe-clipped at nearby study sites while others were unmarked; the unmarked voles were not toe-clipped before removal. Removed animals were released on the opposite side of an interstate highway, approximately 1 km from the study sites. At each capture we recorded species, grid station, individual identification, body mass to the nearest 1 g, sex, and reproductive condition (males, testes abdominal or scrotal; females, vagina open or closed; lactating; pregnant as determined by palpation). All procedures were approved by the University of Illinois Laboratory Animal Care Committee and meet the current guidelines recommended by the American Society of Mammalogists (Gannon *et al.* 2007).

Data analysis

We grouped animals by age based on body mass: adult, ≥ 30 g; juvenile, ≤ 29 g (Hasler 1975). Individuals weighing ≥ 30 g when first captured were assumed to have been born elsewhere and to have immigrated into the site since the last monthly trapping session (Getz *et al.* 2005). All age classes, including immigrants the previous month, were used to estimate total population densities. At removal sites, all individuals of the species to be removed, irrespective of age, were removed from the sites each trapping session. Removed individuals that weighed ≤ 29 g were presumed to have been born in the study site to pregnant females that immigrated into the site soon after the previous trapping session. Of the removed individuals, only adults were considered immigrants. We recognize, however, that a few individuals born on the study site may have exceeded 29 g before the next trapping session. We used ≥ 30 g to designate immigrants because it has been used with one of these species before (eg, Dueser *et al.* 1981), and with both species in our previous study of immigration (Getz *et al.* 2005). Seasonal analyses were based on the following categories: winter (December–February) and spring-autumn (March–November). We adjusted number of immigrants per month into the BGCont site (0.8 ha) to number per ha to be comparable to the other sites.

We compared immigrants at removal sites with those at control sites with respect to body mass and reproductive condition. We used nonparametric Mann-Whitney *U*-tests to compare body mass of immigrants at removal and control sites, and Chi-Square tests to determine whether the proportion of immigrants reproductive differed between removal and control sites, and whether sex ratios of immigrants differed from parity.

We used estimates of population density reported by Getz *et al.* (2001) for the same study areas and same time periods in our multivariate analyses of the effects of population density on immigration. These estimates were used for the species remaining at removal sites and for both species at control sites. Because individuals of the removed

species were immigrating into the removal site during the month, population densities of the removed species obviously were not zero at all times in the removal site. We therefore included density data of the removed species in our multivariate analyses. In order to be consistent with estimates of densities of the non-removed and control populations, we used the total number of individuals (including all age classes) removed in a given month as the population density of the removed species for that month. We estimated general densities of each species in the overall study area by averaging the monthly population densities of all study sites (Getz *et al.* 2001; Fig. 1 in Getz *et al.* 2005).

Using standard linear models to analyze the effects of population density on number of immigrants can be inappropriate because monthly estimates of population densities may be autocorrelated. Thus, we used general linear models with autocorrelated error structure (implemented using GLIMMIX procedure in SAS; SAS Inc., Cary, North Carolina) to test for the effects of density variables (population density of conspecifics or heterospecifics within the site and in the general study area) on the number of immigrants per month arriving at a site. We include scatter plots depicting number of immigrants per month in relation to density at destination sites for significant effects only.

Results

Numbers and physical characteristics of *Microtus ochrogaster* immigrants at removal and control sites

We captured 525 *M. ochrogaster* immigrants (300 males and 225 females) at the site from

which conspecifics had been removed (BGMp, 1977–1987) and 388 immigrants (218 males and 170 females) at the control site (BGCont, 1977–1987). Sex ratios of *M. ochrogaster* immigrants at the removal and control sites were male-biased (site from which conspecifics had been removed, BGMp, 0.57 males; $\chi^2 = 10.71$, $p = 0.001$; control site, BGCont, 0.56 males; $\chi^2 = 5.94$, $p = 0.015$). *M. ochrogaster* immigrants at removal and control sites were similar with respect to body mass and proportion reproductive during winter and spring-autumn (Table 1).

We captured 687 *M. ochrogaster* immigrants (360 males and 327 females) at the site from which heterospecifics had been removed (BGMo, 1977–1997) and 719 immigrants (386 males and 333 females) at the control sites (BGCont, 1977–1987, and BGMp, 1987–1997). The sex ratio of *M. ochrogaster* immigrants at the site from which heterospecifics were removed (BGMo) did not differ from parity (0.52 males; $\chi^2 = 1.59$, $p = 0.21$); however, the sex ratio of *M. ochrogaster* immigrants at the control sites (BGCont and BGMp) was male-biased (0.54 males; $\chi^2 = 3.91$, $p = 0.048$). *M. ochrogaster* immigrants at removal and control sites were similar with respect to body mass and proportion reproductive during winter and spring-autumn (Table 2).

Table 1. Characteristics of *Microtus ochrogaster* immigrants at sites from which conspecifics were either removed or not removed from 1977–1987. Numbers of individuals for which data were available are shown in parentheses. Mann-Whitney *U*-test was used for comparisons of body mass and χ^2 for comparisons of proportion reproductive.

Characteristic	Conspecifics removed (BGMp site)	Conspecifics not removed (BGCont site)	Statistic	<i>p</i> value
Male body mass (g)				
Winter	36.6 ± 0.6 (99)	35.1 ± 0.5 (46)	−0.88	0.38
Spring-autumn	37.0 ± 0.4 (200)	36.2 ± 0.4 (172)	−1.19	0.23
Female body mass (g)				
Winter	35.3 ± 0.6 (62)	36.2 ± 1.0 (33)	−0.58	0.56
Spring-autumn	39.4 ± 0.6 (147)	39.2 ± 0.6 (127)	−0.37	0.71
Proportion of males reproductive				
Winter	0.51 (83)	0.38 (47)	1.84	0.18
Spring-autumn	0.93 (176)	0.88 (169)	3.09	0.08
Proportion of females reproductive				
Winter	0.39 (70)	0.47 (34)	0.65	0.42
Spring-autumn	0.77 (154)	0.77(131)	0.002	0.96

Effects of population density on number of *Microtus ochrogaster* immigrants at removal and control sites

Population density of *M. ochrogaster* positively influenced the number of *M. ochrogaster* immigrants at sites from which conspecifics were experimentally removed (Table 3, part a; Fig. 1a) and at the control site (Table 3, part b; Fig. 1b). No other density variables significantly influenced the number of *M. ochrogaster* immigrants at either the conspecific removal site (Table 3, part a) or the control site (Table 3, part b).

Population density of *M. ochrogaster* positively influenced the number of *M. ochrogaster* immigrants at the site from which *M. pennsylvanicus* were experimentally removed (Table 3, part c; Fig. 1c) and at the control site (Table 3, part d; Fig. 1d). No other density variables significantly influenced the number of *M. ochrogaster* immigrants at either the heterospecific removal site (Table 3, part c) or the control site (Table 3, part d).

Numbers and physical characteristics of *Microtus pennsylvanicus* immigrants at removal and control sites

We captured 835 *M. pennsylvanicus* immigrants (431 males and 404 females) at the site

from which conspecifics had been removed (BGMo, 1977–1997) and 535 immigrants (286 males and 249 females) at the control sites (BGCont, 1977–1987, and BGMp, 1987–1997). Sex ratios of *M. pennsylvanicus* immigrants at the two sites did not differ from parity (site from which conspecifics had been removed, BGMo, 0.52 males; $\chi^2 = 0.87$, $p = 0.35$; control sites, BGCont and BGMp, 0.54 males; $\chi^2 = 2.56$, $p = 0.11$). In winter, body mass of male and female immigrant *M. pennsylvanicus* captured at the site from which conspecifics had been removed was greater than that at the control sites (Table 4). During spring-autumn, body mass of male immigrants was similar at the two sites; but females were slightly heavier at control sites than at the removal site (Table 4). *M. pennsylvanicus* immigrants at the two sites were similar with respect to proportion reproductive during winter and spring-autumn (Table 4).

We captured 380 *M. pennsylvanicus* immigrants (190 males and 190 females) at the site from which heterospecifics had been removed (BGMp, 1977–1987) and 386 immigrants (207 males and 179 females) at the control site (BGCont, 1977–1987). Sex ratios of *M. pennsylvanicus* immigrants at the two sites did not differ from parity (site from which heterospecifics

Table 2. Characteristics of *Microtus ochrogaster* immigrants at sites from which heterospecifics (*M. pennsylvanicus*) were either removed or not removed from 1977–1997. Numbers of individuals for which data were available are shown in parentheses. Mann-Whitney *U*-test was used for comparisons of body mass and χ^2 for comparisons of proportion reproductive.

Characteristic	Heterospecifics removed (BGMo site)	Heterospecifics not removed (BGCont site, then BGMp site)	Statistic	<i>p</i> value
Male body mass (g)				
Winter	37.3 ± 0.6 (86)	35.7 ± 0.5 (80)	-1.67	0.10
Spring-autumn	36.8 ± 0.3 (256)	36.7 ± 0.3 (302)	-0.02	0.98
Female body mass (g)				
Winter	34.5 ± 0.5 (62)	35.9 ± 0.9 (43)	-1.27	0.20
Spring-autumn	39.3 ± 0.4 (265)	38.6 ± 0.4 (283)	-1.14	0.26
Proportion of males reproductive				
Winter	0.48 (93)	0.41 (83)	1.003	0.32
Spring-autumn	0.92 (263)	0.91 (306)	0.260	0.61
Proportion of females reproductive				
Winter	0.36 (67)	0.36 (53)	0.001	0.98
Spring-autumn	0.82 (213)	0.79 (299)	0.639	0.42

Table 3. Analysis of factors influencing density of immigrant *Microtus ochrogaster* (*Mo*) under various removal treatments and controls. Numerator and denominator degrees of freedom, values of F statistics (*F*), and observed significance levels (*p*) are presented.

Effect	Numerator df	Denominator df	<i>F</i>	<i>p</i> value
(a) Response variable: Density of <i>Mo</i> immigrants				
Site: Conspecifics removed (BGMp)				
<i>Mp</i> population density on site	1	69.41	0.18	0.67
<i>Mo</i> population density on site	1	104.40	673.41	< 0.0001
<i>Mo</i> population density in general area	1	86.39	0.24	0.63
<i>Mp</i> population density in general area	1	73.31	0.01	0.93
(b) Response variable: Density of <i>Mo</i> immigrants				
Site: Conspecifics not removed (BGCont)				
<i>Mp</i> population density on site	1	48.38	0.02	0.88
<i>Mo</i> population density on site	1	111.40	18.88	< 0.0001
<i>Mo</i> population density in general area	1	113.80	0.71	0.40
<i>Mp</i> population density in general area	1	51.42	0.01	0.91
(c) Response variable: Density of <i>Mo</i> immigrants				
Site: Heterospecifics removed (BGMo)				
<i>Mp</i> population density on site	1	174.20	0.75	0.39
<i>Mo</i> population density on site	1	181.50	74.56	< 0.0001
<i>Mo</i> population density in general area	1	175.20	0.06	0.80
<i>Mp</i> population density in general area	1	79.01	0.45	0.51
(d) Response variable: Density of <i>Mo</i> immigrants				
Site: Heterospecifics not removed (BGCont, then BGMp)				
<i>Mp</i> population density on site	1	88.56	0.19	0.67
<i>Mo</i> population density on site	1	201.80	24.72	< 0.0001
<i>Mo</i> population density in general area	1	205.70	2.31	0.13
<i>Mp</i> population density in general area	1	88.89	0.37	0.54

were removed, BGMp, 0.50 males; control site, BGCont, 0.54 males; $X^2 = 2.03$, $p = 0.15$). Except for slightly heavier females at the heterospecific removal site in winter, *M. pennsylvanicus* immigrants at the two sites were similar with respect to body mass (Table 5). *M. pennsylvanicus* immigrants at the two sites were similar with respect to proportion reproductive during winter and spring-autumn (Table 5).

Effects of population density on number of *Microtus pennsylvanicus* immigrants at removal and control sites

Population density of *M. pennsylvanicus* positively influenced the number of *M. pennsylvanicus* immigrants at the site from which con-

specifics were experimentally removed (Table 6, part a; Fig. 2a) and at the control site (Table 6, part b; Fig. 2b). No other density variables significantly influenced the number of *M. pennsylvanicus* immigrants at either the conspecific removal site (Table 6, part a) or the control site (Table 6, part b).

Population density of *M. pennsylvanicus* significantly influenced the number of *M. pennsylvanicus* immigrants at the site from which *M. ochrogaster* were experimentally removed (Table 6, part c; Fig. 2c) and at the control site (Table 6, part d; Fig. 2d). No other density variables significantly influenced the number of *M. pennsylvanicus* immigrants at either the heterospecific removal site (Table 6, part c) or the control site (Table 6, part d).

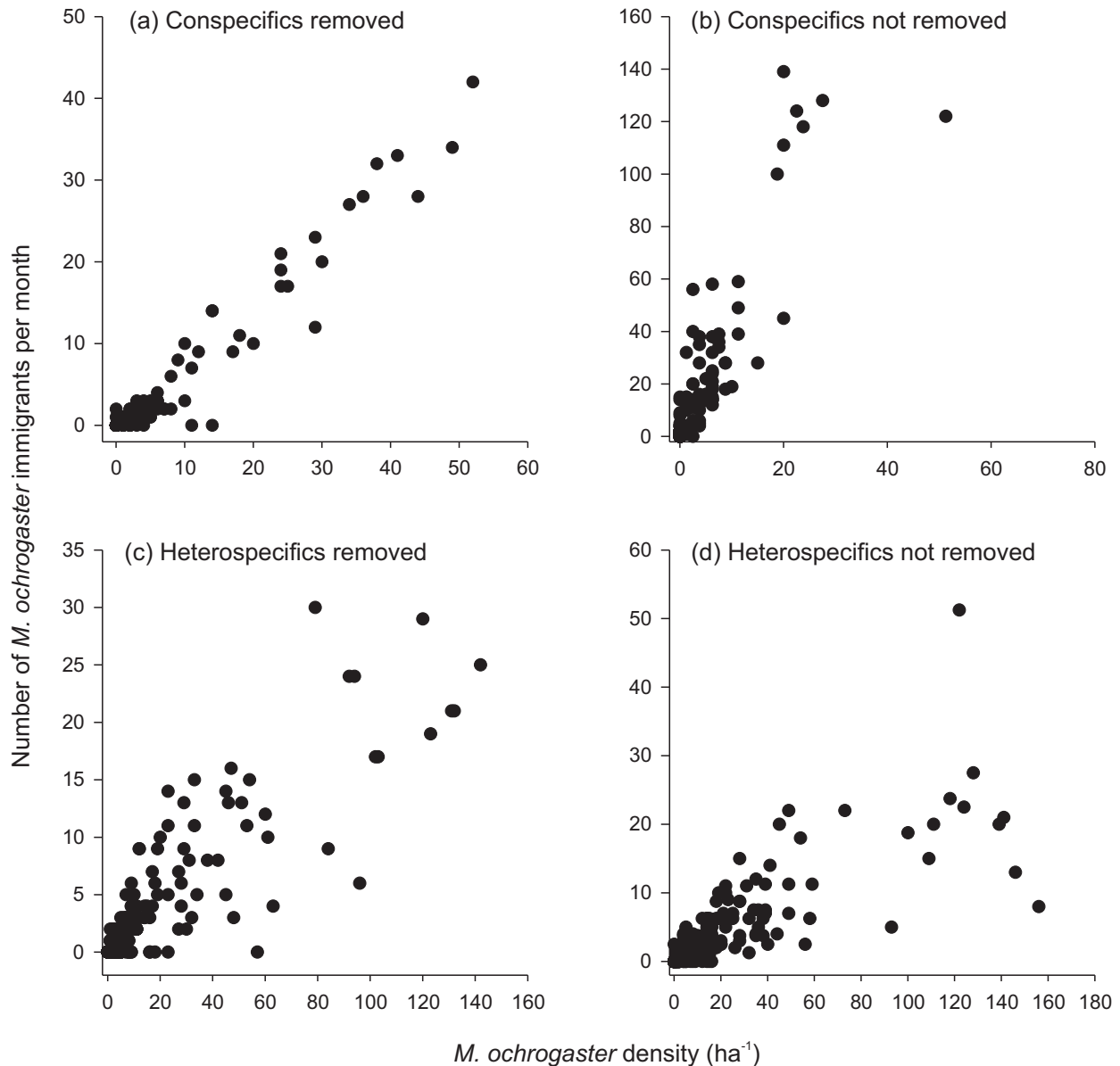


Fig. 1. Relationship between rate of immigration (number of immigrants per month) into a site and population density of conspecifics at that site for *Microtus ochrogaster*. (a) Site at which conspecifics were removed (BGMp). (b) Control site at which no individuals of either species were removed (BGCont). (c) Site at which heterospecifics (*Microtus pennsylvanicus*) were removed (BGMo). (d) Control site at which no individuals of either species were removed (BGCont, then BGMp).

Discussion

Although we captured more male than female immigrants of *Microtus ochrogaster* and *M. pennsylvanicus* at almost all of our sites (at 1 site we captured the same number of male and female immigrants of *M. pennsylvanicus*), only

for *M. ochrogaster* did the sex ratio of immigrants deviate significantly from parity (at 3 of 4 study sites). Occurrence of both males and females among immigrants, and a male-bias where deviations from parity existed, agree with previous descriptions of immigrants for *M. ochrogaster* and *M. pennsylvanicus* (Gaines *et al.*

Table 4. Characteristics of *Microtus pennsylvanicus* immigrants at sites from which conspecifics were either removed or not removed from 1977–1997. Numbers of individuals for which data were available are shown in parentheses. Mann-Whitney *U*-test was used for comparisons of body mass and χ^2 for comparisons of proportion reproductive.

Characteristic	Conspecifics removed (BGMo site)	Conspecifics not removed (BGCont site, then BGMp site)	Statistic	<i>p</i> value
Male body mass (g)				
Winter	37.1 ± 0.6 (87)	33.5 ± 0.4 (54)	−4.54	< 0.001
Spring-autumn	40.6 ± 0.4 (320)	40.5 ± 0.4 (222)	−0.10	0.92
Female body mass (g)				
Winter	36.1 ± 0.7 (52)	32.7 ± 0.3 (71)	−4.39	< 0.001
Spring-autumn	38.1 ± 0.4 (307)	39.2 ± 0.5 (164)	−2.08	0.04
Proportion of males reproductive				
Winter	0.36 (67)	0.18 (33)	3.275	0.07
Spring-autumn	0.92 (333)	0.93 (252)	1.244	0.26
Proportion of females reproductive				
Winter	0.33 (73)	0.23 (22)	0.807	0.37
Spring-autumn	0.68 (314)	0.75 (226)	3.214	0.07

Table 5. Characteristics of *Microtus pennsylvanicus* immigrants at sites from which heterospecifics (*M. ochrogaster*) were either removed or not removed from 1977–1987. Numbers of individuals for which data were available are shown in parentheses. Mann-Whitney *U*-test was used for comparisons of body mass and χ^2 for comparisons of proportion reproductive.

Characteristic	Heterospecifics removed (BGMp site)	Heterospecifics not removed (BGCont site)	Statistic	<i>p</i> value
Male body mass (g)				
Winter	37.7 ± 1.9 (16)	34.2 ± 1.3 (16)	−1.33	0.18
Spring-autumn	37.6 ± 0.5 (132)	38.5 ± 0.4 (191)	−1.59	0.11
Female body mass (g)				
Winter	36.4 ± 1.0 (28)	33.5 ± 0.9 (17)	−2.04	0.04
Spring-autumn	36.9 ± 0.5 (107)	36.8 ± 0.4 (160)	−0.59	0.53
Proportion of males reproductive				
Winter	0.28 (18)	0.19 (16)	0.42	0.52
Spring-autumn	0.87 (128)	0.92 (191)	2.19	0.14
Proportion of females reproductive				
Winter	0.44 (27)	0.23 (13)	1.74	0.19
Spring-autumn	0.74 (102)	0.70 (166)	0.66	0.42

1979, Dueser *et al.* 1981, Baird and Birney 1982, Pugh and Tamarin 1991, Getz *et al.* 2005) and for other species of voles (*Microtus townsendii*,

Lambin 1994, *Microtus arvalis*, Schweizer *et al.* 2007, *Myodes glareolus* and *Microtus agrestis*, Viitala *et al.* 1994).

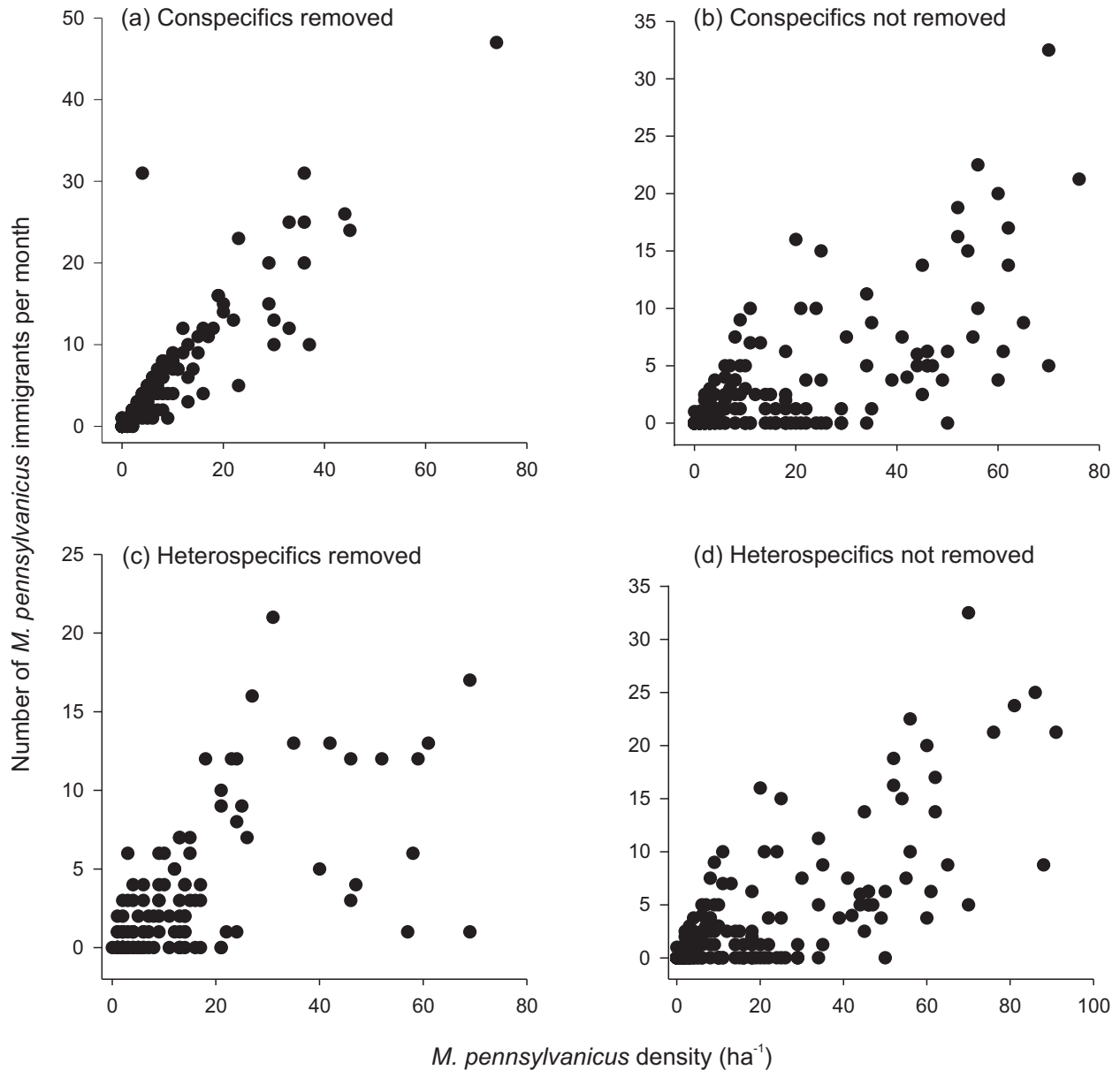


Fig. 2. Relationship between rate of immigration (number of immigrants per month) into a site and population density of conspecifics at that site for *Microtus pennsylvanicus*. (a) Site at which conspecifics were removed (BGMo). (b) Control site at which no individuals of either species were removed (BGCont, then BGMp). (c) Site at which heterospecifics (*Microtus ochrogaster*) were removed (BGMp). (d) Control site at which no individuals of either species were removed (BGCont).

We found that immigrants moving into sites where either conspecifics or heterospecifics had been removed were very similar to immigrants moving into control sites with respect to physical condition. We detected no differences in reproductive condition between immigrants into removal and control grids; this characterized

M. ochrogaster and *M. pennsylvanicus*, males and females, during winter and spring-autumn. Most comparisons of body mass also revealed no differences between immigrants into control and removal sites. The few exceptions concerned *M. pennsylvanicus*: in two cases, male and female immigrants at removal sites during the winter

Table 6. Analysis of factors influencing density of immigrant *Microtus pennsylvanicus* (*Mp*) under various removal treatments and controls. Numerator and denominator degrees of freedom, values of F statistics (*F*), and observed significance levels (*p*) are presented.

Effect	Numerator df	Denominator df	<i>F</i>	<i>p</i> value
(a) Response variable: Density of <i>Mp</i> immigrants				
Site: Conspecifics removed (BGMo)				
<i>Mp</i> population density on site	1	156.40	654.98	< 0.0001
<i>Mo</i> population density on site	1	162.70	0.10	0.76
<i>Mo</i> population density in general area	1	159.00	0.02	0.88
<i>Mp</i> population density in general area	1	92.75	0.11	0.75
(b) Response variable: Density of <i>Mp</i> immigrants				
Site: Conspecifics not removed (BGCont, then BGMp)				
<i>Mp</i> population density on site	1	97.85	114.01	< 0.0001
<i>Mo</i> population density on site	1	229.40	1.48	0.22
<i>Mo</i> population density in general area	1	232.50	0.78	0.38
<i>Mp</i> population density in general area	1	99.49	0.05	0.82
(c) Response variable: Density of <i>Mp</i> immigrants				
Site: Heterospecifics removed (BGMp)				
<i>Mp</i> population density on site	1	50.75	31.45	< 0.0001
<i>Mo</i> population density on site	1	114.40	0	0.99
<i>Mo</i> population density in general area	1	87.12	0.03	0.85
<i>Mp</i> population density in general area	1	53.26	0.09	0.77
(d) Response variable: Density of <i>Mp</i> immigrants				
Site: Heterospecifics not removed (BGCont)				
<i>Mp</i> population density on site	1	51.20	55.00	< 0.0001
<i>Mo</i> population density on site	1	115.90	0.34	0.56
<i>Mo</i> population density in general area	1	109.90	0.02	0.88
<i>Mp</i> population density in general area	1	53.21	0.04	0.84

were heavier than those at control sites (mean body mass differed by 3–4 g); a third involved slightly heavier (≈ 1 g) females into the control than into the conspecific removal site during spring-autumn. In the fourth case, involving female *M. pennsylvanicus* in winter, immigrants into heterospecific removal sites were ≈ 1 g heavier than those at control sites. These observations disagree with Danielson *et al.* (1986) who predicted that immigrants into established populations might be relatively larger, given the presumed difficulty of settling in a population of unfamiliar and potentially aggressive residents.

Dispersing *M. ochrogaster* and *M. pennsylvanicus* responded in a similar manner to population densities of conspecifics at control and removal sites. For both species, the density of

conspecifics at a site positively influenced rate of immigration into that site. These patterns for bluegrass habitat agree with those found for each species in unmanipulated populations in alfalfa, bluegrass, and tallgrass habitats at our general study area (Getz *et al.* 2005) and with those of Meserve and Klatt (1985) for *M. pennsylvanicus* and Diffendorfer *et al.* (1995) for *M. ochrogaster*. However, our findings differ from those of Danielson and Gaines (1987), Lin and Batzli (2001b), and Smith and Batzli (2006), all of whom found a negative correlation between immigration and population density of conspecifics at the site when studying either one or both of these species. Reed and Slade (2008) also found a negative relationship between population density and recruitment (a combined mea-

sure of immigration of adults and recruitment of young) for *M. ochrogaster*. Because these studies differed in type of habitat, duration of monitoring, definition of dispersers, and whether study populations were open with natural immigration or enclosed with experimental immigration (ie, individuals were introduced into enclosures), the precise reasons for the different findings are unclear. In at least one other rodent species (*Peromyscus leucopus*), studies of natural versus experimental immigration have yielded different findings (Seamon and Adler 1997).

Studies across a range of taxa have suggested several potential advantages to selecting habitats that contain conspecifics, including reduced risk of predation and increased access to mates or extra-pair partners (studies reviewed in Stamps 2001). It is also possible that dispersers searching for suitable habitats use conspecifics as an indicator of habitat quality, and that this reduces the costs of habitat selection by reducing time spent searching for a new habitat (Stamps 2001). The precise benefits of settling near conspecifics remain to be determined for our two study species.

In our study, density of heterospecifics at a site did not influence rate of immigration into that site for either *M. ochrogaster* or *M. pennsylvanicus*. Although not directly comparable to our study of open populations with natural immigration, enclosure experiments by Lin and Batzli (2001a) with these same two species revealed only limited effects of heterospecifics on habitat selection. These authors released *M. pennsylvanicus* and *M. ochrogaster* into enclosures either alone or in the presence of the other species, and allowed them to select among habitats that differed in amount of cover and quality of food. Density and demography of each species were not negatively affected by density of the other species, suggesting weak effects of interspecific competition. Nevertheless, *M. pennsylvanicus* influenced movement patterns of *M. ochrogaster*. Specifically, *M. pennsylvanicus* reduced colonization of high quality habitats by *M. ochrogaster* and increased dispersal by *M. ochrogaster* into low quality habitats. These effects were observed only after population densities had increased in the weeks following release of voles into enclo-

tures. Reciprocal effects of prairie voles on *M. pennsylvanicus* were not detected. In another study using field enclosures, presence of *Synaptomys cooperi* negatively impacted colonization by *M. ochrogaster*, but presence of *Sigmodon hispidus*, a recent arrival in the region, had no effect (Danielson and Gaines 1987). Similarly, *M. pennsylvanicus* was a recent arrival in our study region (Getz *et al.* 2001), and we found their presence to have no effect on immigration by *M. ochrogaster*.

In summary, we found little evidence for either *M. ochrogaster* or *M. pennsylvanicus* that individuals moving into occupied bluegrass sites differed in physical condition from those moving into unoccupied (or very low population density) bluegrass sites. For both species, rate of immigration into a site was positively correlated with density of conspecifics at the site, suggesting dispersers were attracted to conspecifics. For both *M. ochrogaster* and *M. pennsylvanicus*, density of heterospecifics at a site did not significantly influence rate of immigration into that site; these findings indicate that dispersers neither avoid nor preferentially settle near heterospecifics during habitat selection. Among studies of habitat selection in diverse taxa, ours is notable in providing data from open populations of 2 closely related species that were continuously monitored for either 10 or 20 years in destination habitats with a wide range of conspecific and heterospecific densities.

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