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RH: Getz et al. — Home ranges of voles

Home range dynamics of sympatric vole populations: influence of food resources, population density, interspecific competition, and mating system

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We studied variation in home range size in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus* in alfalfa, bluegrass and tallgrass habitats over a 25-year period in east-central Illinois. The three habitats differed in food availability and vegetative cover. Home range indices of both species were complexly related to abundance of food resources. Home ranges of *M. ochrogaster* were smallest in the high food habitat (alfalfa), largest in the low food habitat (tallgrass) and intermediate in medium food habitat (bluegrass). *M. pennsylvanicus* home ranges were largest in the low food habitat, but did not differ between the high and intermediate food habitats. *M. ochrogaster* did not have smaller home ranges in supplementally fed medium and low food habitats; those of *M. pennsylvanicus* were smaller only in the low food habitat. Home ranges of *M. ochrogaster* were compressed only at population densities above 100/ha, irrespective of food levels; those of *M. pennsylvanicus* were smaller at high densities only in medium and low food habitats. Presence of the other species did not influence size of home ranges of either species. Within-habitat seasonal variation in home range indices indicated a confounding response to cover (prey risk) and food. Home ranges of all age classes of *M. pennsylvanicus* were larger than those of *M. ochrogaster* in all three habitats. There was no obvious relationship between home range sizes of adult males and females in relation to the mating system of each species. For both species in all three habitats, home ranges of adult males were larger than those of adult females.

Key words: home range, *Microtus ochrogaster*, *Microtus pennsylvanicus*, voles

An understanding of variation in home range size of small mammals, and factors responsible for such variation, is important to demographic studies within and among habitats. The manner in which individuals respond to environmental influences by increasing or decreasing their range of movements provides evidence for the role of given variables in demography of species. A number of factors potentially influence the area over which an individual moves in its day-to-day activities, i.e., its home range. Variation in distribution and abundance of food and other resources (e.g., cover, nest sites) may influence habitat-specific and seasonal differences in size of home ranges.

At higher population densities, competition for space and resources may result in compression of home range size (Mares et al. 1982; Vincent et al. 1995; Oli et al. 2002). When two competing species occupy a site, interspecific interactions may result in contraction of home ranges of one or both species.

The amount of area over which an individual must range to obtain sufficient food is an especially important determinant of home range size for many species (Meserve 1971; Slade et al. 1997; Abramsky and Tracy 1980; Taitt and Krebs 1981; Ims 1987; Mares and Lacher 1987; Boutin 1990; Desy et al. 1990; Jones 1990; Akbar and Gorman 1993; Fortier and Tamarin 1998; Fortier et al. 2001). Further, several studies have shown that as population density changes, presumably altering levels of competition for space and resources, so too may home range size (Abramsky and Tracy 1980; Gaines and Johnson 1982; Rodd and Boonstra 1984; Ostfeld and Canham 1995; Fortier and Tamarin 1998; Hubbs and Boonstra 1998). However, other studies (Lacki et al. 1984; Wolff 1985; Mares and Lacher 1987) found no such relationship between food availability and population density.

Anderson (1986) and Desy et al. (1990) found home ranges of some species of arvicoline rodents to be smaller in sites where the risk of predation is greater, i.e., habitats with sparse cover.

Schmidt et al. (2002) reported a positive relationship between home range size male, but not female, body mass in *Dicrostonyz groenlandicus*. However, food availability confounded the relationship between body mass and home range size of females.

Home range size also may vary with reproductive tactics of the sexes. Gaulin and Fitzgerald (1988) found that in species displaying promiscuous/polygynous mating systems (e.g., *Microtus pennsylvanicus*), males had larger home ranges than did females, owing to male-male competition for mates. They further found that home range sizes did not differ between the sexes in monogamous/communal nesting species (e.g., *M. ochrogaster*). On the other hand, Meserve (1971) and Swihart and Slade (1989) found home ranges of male *M. ochrogaster* to be larger than those of females. Getz et al. (1993) reported that 45% of the adult males in *M. ochrogaster* populations were not residents at nests of male-female pairs or communal groups, and wandered within the study site. Inclusion of these males in the analyses may result in biased results regarding home range sizes of male *M. ochrogaster*.

Reliable estimates of small mammal home ranges are difficult to achieve. Considerable effort is required to delimit precisely the boundaries of the area an individual occupies, whether by indirect measures such as radio telemetry or by direct observation (Jones and Sherman 1983; Ribble et al. 2002). A commonly employed alternative method of estimating home range size includes plotting capture locations from grid live-trapping and estimating the area encompassed by the study animals (Hayne 1949, 1950). Because grid stations do not correspond to the boundaries of individual home ranges, considerable

variability is inherent in such measures. All too often, trapping protocols result in only 3-5 captures of a given individual, rendering such data more or less anecdotal (Krohne 1986). Less precise indirect means of estimating home range size include measuring distances between captures, either between the first two captures or the maximum distance between all captures during a given trapping session (Gaines and Johnson 1982 Slade and Swihart 1983; Slade and Russell 1998). Because most field studies of arvicoline rodents are of limited duration (1-5 years; Taitt and Krebs 1985), the quantity of data available for estimating home ranges is limited. Small sample sizes, combined with the imprecision of estimates and variability in home range size, limit analyses of home range data.

In this paper we present home range data obtained during the course of a 25-year study of the prairie vole, *Microtus ochrogaster*, and meadow vole, *M. pennsylvanicus* (Getz et al. 2001). Populations of the two species in three different habitats were monitored monthly, year-round. The habitats differed in food availability and seasonal changes in cover. As a result of the scope and duration of the study, we obtained sufficiently large sample sizes of home range indices (*M. ochrogaster*, >12,000; *M. pennsylvanicus*, >5,000) to test hypotheses regarding variation in home range size and demographic implications. In addition, we analyzed home range data from two shorter term manipulative studies involving supplemental feeding and interspecific interactions.

We tested the following predictions: (1) home ranges are smaller where (habitats) and when (seasons) food is more abundant, (2) there is a negative relationship between home range size and population density, (3) interspecific competition between two sympatric species will result in smaller home ranges of one or both, (4) home range sizes will be

smaller when risk of predation is greatest, and (5) home ranges reflect mating tactics of the species. We also evaluated the importance of variation in home range size in understanding the demography of the two species.

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). For the long term study, populations of *M. ochrogaster* and *M. pennsylvanicus* were monitored monthly in 3 habitats: restored tallgrass prairie (March 1972--May 1997), bluegrass, *Poa pratensis* (January 1972--May 1997), and alfalfa, *Medicago sativa* (May 1972--May 1997; Getz et al. 1987, 2001). Tallgrass prairie was the original habitat of both species in Illinois, and bluegrass, an introduced species, represents 1 of the more common habitats in which the 2 species can be found today in Illinois. Alfalfa is an atypical habitat that provides exceptionally high-quality food for both species (Cole and Batzli 1979; Lindroth and Batzli 1984).

We trapped study sites in 2 restored tallgrass prairies, 1 located in Trelease Prairie, the other in Phillips Tract (Getz et al. 1987). Trelease Prairie, established in 1944, was bordered by a mowed lawn, cultivated fields, a forest, 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%); *Poa 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. The site was bordered on 1 side by an abandoned field that underwent succession from forbs and grasses to shrubs and small trees by the time the study ended. Cultivated fields bordered the other 3 sides. When the Phillips Tract site was first trapped in September 1977, prairie vegetation was well-developed. Lindroth and 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 retard invading shrubs and trees.

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

To reduce successional changes, especially invading forbs, shrubs and trees, the bluegrass sites were mowed during late summer every 2-3 years. The entire area was mowed at the same time. A rotary mower was set to cut the vegetation about 25 cm above the surface. That height resulted in suppression of growth of the invading forbs and woody vegetation, but left the bluegrass uncut.

Two adjacent sites with *M. sativa* were trapped during the study. A site was trapped until the *M. sativa* began to be crowded out by invading forbs and grasses. One year before trapping was terminated in 1 site, *M. sativa* was planted in the other site so that the plants

would be fully developed when trapping commenced in that site. Sites were separated by a 10-m closely mown strip. The strip reduced the incidence of animals having home ranges that included parts of the two study ssites when *M. sativa* was present in both fields. Initially, *M. sativa* comprised 75% of the vegetation in each site. During the last year of usage, other common plants included *P. pratensis*, *Solidago*, *Phleum pratense*, *Bromus inermis*, clover (*Trifolium repens* and *T. pratense*), and plantain (*Plantago*). A series of 3-m wide strips were mowed (every 3rd strip) 25 cm above the surface periodically each summer to control invading weedy forbs and promote new growth of *M. sativa*. The first strips usually were mowed in early June; mowing normally stopped in mid September. The subsequent strips were not mowed until vegetation in the previously mowed strips was nearly full-grown. Times of mowing were spaced so that at least two-thirds of the field had vegetative cover at all times.

Trapping procedures.--A grid system with 10-m intervals was established in all study sites. 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 the traps. We used vegetation or aluminum shields to protect the traps from the sun during the summer. The wooden traps provided ample insulation in the winter making provision of nesting material unnecessary. We estimated trap mortality to be less than 0.5% during the study.

Traps were set in the afternoon and checked at approximately 0800 h and 1500 h the following 3 days. All animals were toe-clipped at first capture for individual identification (maximum of 2 toes on each foot). 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, and body mass to the nearest 1 g were recorded at each capture. For analysis, animals were grouped by age based on body mass: $\geq$ 30 g, adult; subadult, 20-29 g; and juvenile, $\leq$ 19 g.

Manipulative studies

We conducted two manipulative studies to examine the influences of food availability and interspecific interactions on demography and population fluctuations of the two species. Home range indices were calculated for these data sets. Trapping procedures were as described above.

Supplemental feeding.--A 0.5 ha bluegrass study site was supplementally fed from June 1977 through December 1983 (Getz et al. 1987). A 0.5 ha tallgrass site was supplementally fed from September 1977 through May 1987. 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 and 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.--Effects of presence of one species on the other were examined in both bluegrass and tallgrass. All *M. pennsylvanicus* were removed from a 1.0 ha bluegrass site each trapping session from May 1977 through May 1997. *M. ochrogaster* were removed from another 1.0 ha bluegrass site from May 1977 through May 1987. Because *M. ochrogaster* populations were very low and *M. pennsylvanicus* very high most of the time in tallgrass (Getz et al. 2001), only effects of the latter on *M. ochrogaster* were tested in tallgrass. *M. pennsylvanicus* were removed from a 0.5 ha tallgrass site from September 1984 through May 1997. All animals removed from a site were released on the opposite side of an Interstate highway, approximately 1 km from the study sites.

Data analysis

We used the minimum number alive method to estimate population density for each trapping session (Krebs 1966). Previously marked individuals not captured in a given trapping session, but captured in a subsequent session, were considered to have been present during the sessions in which they were not captured. Although the Jolly-Seber index is recommended for estimating population density (Efford 1992), at least 10 individuals must be trapped each session in order to obtain reasonable estimates (Pollock, et al. 1990). During months voles were present in the study sites, 10 or fewer *M. ochrogaster* were trapped 26%, 52% and 62% percent of trapping sessions in alfalfa, bluegrass, and tallgrass, respectively. Ten or fewer *M. pennsylvanicus* were trapped 55% of the sessions in alfalfa, 46% in bluegrass, and 24% in tallgrass. Since the same index should be used throughout, we felt justified in using MNA. Further, since 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 the *M. ochrogaster* and 91% of the *M. pennsylvanicus* were captured each session.

We calculated home range indices from the distances (in meters) between the first two captures of individuals caught two or more times during a 3-day trapping session (Gaines and Johnson 1982; Slade and Swihart 1983). For comparing home range indices among habitats, we analyzed home range indices for total adults, adult males and females, subadults, and juveniles. Because of small sample sizes for subadults and juveniles, all other comparisons involved only adult males and females.

Seasonal analyses of home range sizes were based on the following categories: spring, March-May; summer, June-August; autumn, September-November; winter, December-February.

We used correlation analyses to investigate the influence of population density on mean monthly home range indices for adult males and females in all three habitats. Except for *M. pennsylvanicus* in tallgrass, population densities were low for extended periods in all three habitats and sample sizes small. Thus, we also tested for effects of population density on home range size by grouping population densities into four categories (1-25/ha, 26-50/ha, 51-100/ha, and $\geq$ 100/ha), and compared home range indices among these categories. Linear regressions were utilized to test relationship between adult body mass and home range indices.

For the period during which voles in experimental plots were supplementally fed, home range indices for the duration of the study were compiled for the experimental and control sites. In the interspecific competition study, populations of the two species fluctuated out of synchrony in the removal and control sites. There

were extensive periods when the "removed" species was also absent from the control site. We therefore compared home range indices for periods when the potentially interfering species was present at population densities above the mean for bluegrass (*M. ochrogaster* 18/ha; *M. pennsylvanicus*, 14/ha; Getz et al. 2001). When this restriction was applied, data were sufficient only for analysis of effects of *M. pennsylvanicus* on home range size of *M. ochrogaster* in manipulated bluegrass sites.

In addition, home range indices from the blue grass habitat of the general study were compared to estimate potential interspecific effects. Home range indices of adult males and females of each species in bluegrass were compared during periods when population densities of the other species were above and below the mean density of that species for bluegrass

Data on resident and non-resident male and female *M. ochrogaster* were compiled from results of a behavioral study conducted in alfalfa habitat from March 1982-May 1987 (Getz et al. 1993). We calculated home range indices for these animals as described above.

Statistical analyses

Because most variables did not meet the requirements for normality (population densities and home range indices were non normal at the 0.05 level; Kolmogorov-Smirnov test, Zar 1999), all variables were log-transformed. Further, because some indices were zero (animals caught at only one station), the data were log (X+1)-transformed because the logarithm of zero is not defined. This allowed us to test for differences using analysis of variance (ANOVA), independent-sample t-tests, or Pearson's correlation coefficient procedures, where appropriate. One-way ANOVAs were followed by Tukey's honestly

significant difference (HSD) post hoc comparisons. Sample sizes for Pearson's correlation coefficient procedures represent the number of months in the sample, whereas those for ANOVA and t-tests represent the number of individual home range indices in the samples. When degrees of freedom (*d.f.*) for t-tests are given in whole numbers, variances were equal (Levene's test for equality of variances). When variances were not equal, *d.f.* is given to one decimal place. We used SPSS 10.0.7 for Macintosh (SPSS, Inc. 2001) for all statistical analyses.

Results

Microtus ochrogaster.--Home range indices for all categories (all adults combined, adult males and females, subadults, and juveniles) averaged over the entire long-term study, were smallest in alfalfa, intermediate in bluegrass and largest in tallgrass. Home range indices in each habitat differed from those in other habitats (Tukey's HSD, <0.05; Table 1). Adult male home ranges were significantly larger than those of adult females in all three habitats (alfalfa: $t = 11.71$, $d.f. = 5478.4$, $P < 0.001$; bluegrass: $t = 5.91$, $d.f. = 2453.4$, $P < 0.001$; tallgrass: $t = 3.62$, $d.f. = 650.2$, $P < 0.001$; Table 1).

Home range indices of adult males were largest during the summer and smallest during winter in alfalfa and bluegrass (Table 2). There was no seasonal difference in adult male home range indices in tallgrass. The only significant seasonal difference in home range size of adult females involved larger indices during autumn than winter in alfalfa. Among habitats, adult male and female indices were significantly smaller in alfalfa than in bluegrass and tallgrass during all seasons (Table 2). The only seasonal difference in home range indices between the latter two habitats was larger adult male home

range indices in tallgrass than in bluegrass during winter (Tukey's HSD, < 0.05).

Population density and home range indices of adult male and female *M. ochrogaster* were not correlated in alfalfa (r = 0.107, N = 213, P = 0.118 and r = 0.099, N = 212, P = 0.153, males and females, respectively). In bluegrass there was a positive correlation between population density and male home range indices (r = 0.242, N = 171, P = 0.001) and a negative correlation for female indices (r = -0.231, N = 160, P = 0.003). Home range indices and population density were not correlated in tallgrass (r = 0.081, N = 90, P = 0.449 and r = 0.051, N = 74, P = 0.663, males and females, respectively). When home range indices were grouped into categories of population density, those of adult males and females in all three habitats were significantly smaller only during periods of very high population density, $\geq$ 101/ha (Table 3).

When compared within habitats over the entire 25 years, body mass and home range indices of both adult male and female *M. ochrogaster* were correlated in alfalfa (r = 0.070, N = 2771, P < 0.001 and r = 0.060, N = 2794, P = 0.001, respectively) and bluegrass (r = 0.074, N = 1938, P = 0.001 and r = 0.053, N = 2018, P = 0.017, respectively). There was no relationship between body mass and home range indices in tallgrass (r = 0.013, N = 947, P = 0.686 and r = 0.042, N = 871, P = 0.218, males and females, respectively). When seasonal comparisons were made of body mass and home range indices within the three habitats, only five (spring, females in bluegrass; summer, males in alfalfa and bluegrass; autumn, males in alfalfa and females in bluegrass) of the 24 possible season x sex x habitat comparisons were significant.

Home range indices of males that were residents at nests of male-female pairs or communal groups were larger than those of female residents (9.1 $\pm$ 1.0 and 5.6 $\pm$ 0.5, respectively; t = 2.726, $d.f.$ = 286.0, P = 0.007). Home range indices of resident males were smaller than those of non resident males that wandered within the study sites (9.1 $\pm$ 1.0 and 15.8 $\pm$ 1.8, respectively; t = 3.631, $d.f.$ = 199.7, P < 0.001).

Microtus pennsylvanicus.--Home range indices of all adults combined and adult females were significantly larger in tallgrass than in alfalfa or bluegrass (Table 1); home range indices did not differ between the latter two habitats. Home range indices of adult males, subadults and juveniles were larger in tallgrass than in bluegrass, but did not differ between tallgrass and alfalfa. Juvenile home ranges were significantly smaller in bluegrass than in alfalfa. Adult male home ranges were larger than those of adult females in all three habitats (Alfalfa: t = 7.17, $d.f.$ = 465.5, P < 0.001; Bluegrass: t = 698, $d.f.$ = 949.4, P < 0.001; Tallgrass: t = 6.80, $d.f.$ = 1026.4, P < 0.001).

Adult male home ranges were significantly smaller in winter than during other seasons in alfalfa and bluegrass (Table 2). In tallgrass, home range indices of adult males were significantly larger during summer-autumn than winter-spring. The only seasonal difference in home range indices of adult females within the three habitats was smaller home ranges during winter than spring in alfalfa.

Although ANOVA analysis indicated there were differences in home range indices among the three habitats for females during spring, and males during summer and winter, HSD tests did not indicate which habitats differed. Pair-wise comparisons of each of the three sets of samples, using 2-sample t-tests, indicated that home range indices

differed between only tallgrass (larger) and bluegrass (smaller). During winter, male home ranges were smallest in alfalfa, but the difference from tallgrass only approached significance (t = 1.898, *d.f.* = 204, P = 0.059). During autumn, home range indices of both males and females were larger in tallgrass than in alfalfa or bluegrass. Home range indices of females during winter were significantly smaller in alfalfa than in either bluegrass or tallgrass.

Home range indices of male, but not female, *M. pennsylvanicus* were positively correlated with population density in alfalfa (r = 0.309, N = 57, P = 0.020 and r = 0.200, N = 62, P = 0.119, males and females, respectively); however home range indices were negatively correlated with population density in tallgrass; those of males approached significance (r = -0.140, N = 177, P = 0.063 and r = -0.194, N = 163, P = 0.013, males and females, respectively). Home range indices and population density were not correlated in bluegrass, although those of females approached significance (r = 0.106, N = 112, P = 0.265 and r = 0.181, N = 111, P = 0.058, males and females, respectively). When grouped by categories of population density, there was no relationship between home range indices and population density of *M. pennsylvanicus* in alfalfa. In bluegrass and tallgrass, home range indices of adult males and females were significantly smaller at the higher densities; those of males became compressed at lower densities in the lower food tallgrass than in bluegrass (Table 3).

The only significant relationship between body mass and home range indices of *M. pennsylvanicus* within habitats over the 25 years was for males in tallgrass (r = 0.101, N = 773, P = 0.005). Of the 24 season x sex x habitat comparisons, only female body mass during winter in bluegrass was significantly negatively related to home range indices.

Interspecific comparisons.--Home range indices of *M. pennsylvanicus* (all adults combined, adult males, adult females) were significantly larger (P <0.001) than those of *M. ochrogaster* in all three habitats (Table 1). The differences were much more pronounced in alfalfa than in bluegrass or tallgrass. Sample sizes of *M. pennsylvanicus* were too small for interspecific comparisons of subadult and juvenile home ranges.

Male *M. pennsylvanicus* home range indices in alfalfa were larger than those of wandering male *M. ochrogaster* (20.3 $\pm$ 1.3 and 15.8 $\pm$ 1.8, respectively; t = 3.135, *d.f.* = 147.9, P = 0.002).

Response to supplemental feeding.--There were no differences in home range indices of adult males or females of either species in supplementally fed and control bluegrass sites (Table 4). There also were no differences in home range indices of adult male and female *M. ochrogaster* in supplementally fed and control tallgrass sites. Home ranges of adult male and female *M. pennsylvanicus*, however, were significantly smaller in supplementally fed than in control tallgrass sites (Table 4).

Seasonal sample sizes (adult males and females, combined) were sufficient for comparison of home ranges in supplementally fed and control sites during the winter only in tallgrass. There was no difference in home range indices of *M. ochrogaster* (12.4 $\pm$ 1.9 and 13. 2 $\pm$ 1.8, supplementally fed and control respectively; t = 0.271, *d.f.* = 85, P = 0.787). Indices for *M. pennsylvanicus* during winter were significantly smaller in the supplementally fed tallgrass site than the control (8.7 $\pm$ 0.9 and 12.9 $\pm$ 1.4, respectively; t = 2.588, *d.f.* = 130.3, P = 0.011).

Interspecific interactions.--Overall, presence of one species had little impact on home range indices of the other species. There was no

difference in the home range indices of adult male and female *M. ochrogaster* when alone and when *M. pennsylvanicus* was present at population densities above the mean density for bluegrass (14/ha) in the control site (male indices: 9.8 ± 1.0 and 10.4 ± 1.6 when alone and in the presence of *M. pennsylvanicus*, respectively, $t = 0.682$, $d.f. = 214$, $P = 0.496$; females: 9.1 ± 1.0 and 7.9 ± 0.8, respectively; $t = 0.861$, $d.f. = 253$, $P = 0.390$). When home range indices were estimated for adult males and females of each species in bluegrass over the entire 25-year period, relative to periods when population density of the other species was below or above the mean for bluegrass, the only significant difference concerned larger indices of female *M. ochrogaster* when densities of *M. pennsylvanicus* were above mean densities (males: 15.2 ± 0.6 and 15.7 ± 1.5; $t = 0.415$, $d.f. = 1227$, $P = 0.678$; females: 10.7 ± 0.5 and 12.4 ± 1.1; $t = 2.747$, $d.f. = 405.4$, $P = 0.006$; below and above the mean, respectively). There was no difference in home range indices of either male or female *M. pennsylvanicus* when densities of *M. ochrogaster* were below or above the mean density for bluegrass (males: 17.6 ± 0.8 and 18.7 ± 1.4; $t = 1.066$, $d.f. = 492$, P = 0.287; females: 11.0 ± 0.5 and 14.5 ± 1.3; $t = 1.680$, $d.f. = 613$, $P = 0.093$).

Discussion

In this study, mean home range indices for *Microtus ochrogaster* among the three habitats suggested home range size was inversely related to food availability. For all sex and age categories, home range indices were smallest in alfalfa (high food habitat), intermediate in bluegrass (intermediate food habitat) and largest in tallgrass (low food habitat). Seasonal comparisons of home range indices of *M. ochrogaster* among the three habitats also reflected the

influence of food availability. Home range indices of adult male and female *M. ochrogaster* were consistently smaller in alfalfa than in bluegrass and tallgrass during all four seasons. Further, indices of adult male home ranges during winter were larger in tallgrass than in bluegrass.

Within-habitat seasonal variation in home range indices of *M. ochrogaster* did not reflect presumed changes in food availability. Food availability was presumed to be lesser during winter than other seasons in all three habitats and greater in alfalfa during winter than in bluegrass or tallgrass (Getz et al. In Review a). Home range indices of adult males, on the other hand, were significantly smaller during winter than other seasons in both alfalfa and bluegrass and there was no seasonal difference in home range indices of males in tallgrass. Home range indices of females did not differ seasonally in any of the three habitats.

The association between food availability and home range indices among the three habitats was less obvious for *M. pennsylvanicus* than for *M. ochrogaster*. Only total adult and adult female home range indices were significantly larger in the low food tallgrass habitat than in high food alfalfa and intermediate food bluegrass. Further, there was no difference between home range indices of adults in intermediate food bluegrass and high food alfalfa. In addition, there were few among-habitat seasonal differences in home range indices of *M. pennsylvanicus* with respect to presumed food availability. As for *M. ochrogaster*, within-habitat seasonal differences in home range indices of *M. pennsylvanicus* were inconsistent in respect to food availability.

Variation in home range indices of *M. ochrogaster* in response to supplemental feeding did not support our predictions. There was no

difference in home range indices of adult males and females in supplementally fed and control sites in bluegrass or tallgrass. Home range indices of both sexes of *M. pennsylvanicus* were smaller in supplementally fed than in control tallgrass but did not differ between supplementally fed and control bluegrass sites. When compared seasonally, home range indices of *M. pennsylvanicus* in the supplementally fed tallgrass site were smaller than those in the control site during all seasons except autumn. However, only the differences during spring were statistically significant. These results suggest that while the abundance of food resources generally may result in smaller home range sizes in *M. pennsylvanicus*, effects of food availability on home range sizes may vary seasonally.

The results from the supplemental feeding study are consistent with demographic responses of the two species to the addition of food to bluegrass and tallgrass sites. Population densities of *M. ochrogaster* did not change in response to supplemental feeding in bluegrass and tallgrass. *M. pennsylvanicus* displayed higher population densities in supplementally fed than control tallgrass, but not in bluegrass sites (Getz et al. 1987, In Review b).

In the manipulative studies, presence of the other species, even at high densities, did not result in differences in home ranges of either *M. ochrogaster* or *M. pennsylvanicus*. This provides additional evidence that there was little relationship between home range size and food availability. Since the two species feed on the same plants, high densities of one species should effectively reduce food availability for the other. Accordingly, one would expect home ranges to be larger, if there was no interspecific social interaction restricting movements of the two species as food availability per individual became less. If interspecific interactions restricted access of individuals of one or

both species to food, smaller home ranges would be displayed by one or both species. However, home range sizes of neither species differed in the presence of the other species.

Although home ranges of *M. ochrogaster* were positively associated with body mass, such a response did not appear related to energy requirements. The positive responses were observed in the higher food habitats, alfalfa and bluegrass, but not in low food tallgrass. Neither did the mating system appear to be involved, as was observed in *Dicrostonyx groenlandicus* (Schmidt et al. 2002).

Our results regarding interactions between home range size and presumed food availability agree only very generally with those of Meserve (1971), Taitt and Krebs (1981), Boutin (1990), Jones (1990), and Fortier and Tamarin (1998), who found home ranges to be smaller where food availability is greater. Our results also do not agree entirely with those of Swihart and Slade (1989), Abramsky and Tracy (1980), Desy et al. (1990), Fortier et al. (2001), in which home range sizes were found to be either the same or smaller in low food sites in comparison to where food was more abundant.

Abramsky and Tracy (1980), Gaines and Johnson (1982), Ostfeld and Canham (1995), and Fortier and Tamarin (1998) have shown home ranges to be compressed as population density and competition for resources increased. Our results indicated such a relationship either was expressed only at very high densities (*M. ochrogaster*) or was not consistent with predicted interactions with food availability (*M. pennsylvanicus*). There was no direct interaction between population density and food availability in relation to home range size of *M. ochrogaster*. Home ranges of both adult males and females became significantly smaller only at population densities $\geq$ 101/ha, irrespective of food availability, suggesting that only very high

population densities result in compression of home ranges. Similarly, variation in home range sizes of *M. pennsylvanicus* did not display an interaction between population density and food availability. Indices of *M. pennsylvanicus* became compressed at lower population densities where food was presumed to be less available, the opposite of what one would anticipate if food were a major determinant of home range size.

We conclude elsewhere that among-habitat differences in demography of *M. ochrogaster* and *M. pennsylvanicus* result from differences in survival related to vegetative cover, not food availability (Getz et al. In Review a). On first appraisal, our analyses of home range indices appear to agree with these conclusions. However, seasonal/habitat differences in home range indices are not entirely consistent with conclusions regarding influence of cover.

Anderson (1986) and Desy et al. (1990) found home ranges of some species of arvicoline rodents to be smaller in sites where the risk of predation is greater, i.e., habitats with sparse cover. Our data suggest a similar response to risk of predation, but the effect is complicated by variation in food availability. Cover was less throughout the year in alfalfa than in either bluegrass or tallgrass and within alfalfa, less during the winter than other seasons; there was little seasonal difference in cover in bluegrass and tallgrass (Getz et al. In Review a). Although lower during winter than other seasons within each of the three habitats, food availability during the winter was greater in alfalfa than in bluegrass or tallgrass.

Overall home range indices of both species varied as would be expected if cover/predation risk were mainly involved, i.e., smaller in alfalfa than in bluegrass and tallgrass. Home range indices of males of both *M. ochrogaster* and *M. pennsylvanicus* were smaller during the winter than other seasons in alfalfa and bluegrass, but not in

tallgrass. This suggests food may be a more important factor than cover in determining home ranges size. On the other hand, home range indices of adult males of both species were smaller in alfalfa during winter when food was comparatively low, than during other seasons, when food was more abundant. This suggests a response to predator risk. There was, however, no difference in home range indices of female *M. ochrogaster* and only a tendency for smaller indices of female *M. pennsylvanicus* during winter in alfalfa than in other seasons. This suggests that, if predation risk were a factor in home range sizes, only males display such a response. Desy et al. (1990) found no such sex differences in relation to prey risk of *M. ochrogaster*.

We found that adult male home range indices of both *M. ochrogaster* (monogamous) and *M. pennsylvanicus* (promiscuous) were greater than those of adult females. Further, males of male-female pairs and communal groups of *M. ochrogaster* had larger home range indices than did resident females. Resient males make brief forays out of the shared home range (Hofmann et al. 1984; Getz et al. 1986; McGuire and Getz 1998; McGuire et al. 1990), and this may contribute to their larger home range indices. On the other hand, resident male *M. ochrogaster* had significantly smaller home range indices than did wandering males, suggesting that the social status of males influences their home range size. Thus, our results agree those of Swihart and Slade (1989) who found male *M. ochrogaster* home ranges to be larger than those of females. Our results agree only partially with those of Gaulin and Fitzgerald (1988) who found home range sizes did not differ between male and female *M. ochrogaster*. That our data were from a high food habitat, while those of the latter two studies were from lower food situations, may confound comparisons.

Home range indices for *M. pennsylvanicus* were larger than those of *M. ochrogaster*. Larger body mass of *M. pennsylvanicus* (Getz et al. In Review a) and presumed greater food requirements may, in part, be involved. One would expect the same relative differences between home range indices of the two species, irrespective of food level, if home range sizes were influenced primarily by food availability. However, differences were greatest in the high food alfalfa habitat, where the home ranges of the two species would be expected to be more similar than where food was less abundant.

It thus appears variation in home range size is complexly involved in demography of *M. ochrogaster* and *M. pennsylvanicus*, and that such interactions vary with species and habitat. Under some circumstances, increased population density may result in smaller home ranges and less food availability to individuals. Under other conditions, however, home ranges are not compressed, except at very high densities, and are not related to food availability.

In conclusion, we found only partial support for our original predictions: (1) there was only a general correlation between food availability and home range sizes, and such agreement was not consistent with seasonal variation in food availability; (2) home range size was compressed only at relatively high densities; (3) there was no effect of interspecific interactions on home range sizes of either species; (4) while risk of predation may have influenced home range size, the effect was confounded by food availability; and (5) there was little correlation between home range sizes of *M. ochrogaster* and *M. pennsylvanicus* that could be explained by species differences in mating system.

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Table 1. Mean home range indices (mean ± SE, in meters) by habitat. Values of *F*-statistic, degrees of freedom, and observed significance level (*P*) for one-way ANOVA comparing home range indices among the three habitats are also given. Values within a *row* with different superscript letters differ significantly at 0.05 level (Tukey's HSD test). Independent-sample t-tests were used to compare paired means of total adult, adult male and adult female *M. ochrogaster* and *M. pennsylvanicus*; paired values in each *column* with different superscript numbers differ at 0.001 level.

	Habitat			*F*; df
	Alfalfa	Bluegrass	Tallgrass	
M. ochrogaster				
Total adults	8.9 ± 0.2^{a1}	13.2 ± 0.4^{b1}	15.5 ± 0.6^{c1}	158.383; 2
Adult males	11.1 ± 0.3^{a1}	15.3 ± 0.6^{b1}	17.5 ± 0.9^{c1}	62.5039; 2
Adult females	6.7 ± 0.2^{a1}	11.2 ± 0.5^{b1}	13.3 ± 0.8^{c1}	108.4464; 2
Subadult	7.7 ± 0.6^{a}	12.2 ± 0.7^{b}	17.7 ± 1.9^{c}	49.4942; 2
Juveniles	5.2 ± 0.3^{a}	8.3 ± 0.8^{b}	13.9 ± 1.4^{c}	34.1321; 2

Table 1 (Cont.)

M. pennsylvanicus				
Total adults	15.6 ± 0.7^{a2}	14.4 ± 0.4^{a2}	18.6 ± 0.6^{b2}	6.053; 2,
Adult males	20.2 ± 1.3^{ab2}	17.7 ± 0.8^{b2}	22.8 ± 1.0^{a2}	6.9803; 2,
Adult females	11.8 ± 0.8^{a2}	11.8 ± 0.4^{a2}	14.4 ± 0.5^{b2}	19.1112; 2
Subadult	14.2 ± 1.8^{ab}	10.7 ± 0.7^{b}	14.2 ± 0.6^{a}	12.8429; 2
Juveniles	14.1 ± 2.6^{a}	8.1 ± 0.8^{b}	13.9 ± 1.4^{a}	8.7809; 2

Table 2. Seasonal home range indices (mean ± SE, in meters). Values of *F*-statistic, degrees of freedom and observed significance level (*P*) for one-way ANOVA comparing home range indices among the four seasons and for sexes among habitats within seasons are also given. Values within a row with different superscript letters differ at 0.05 level; values for each sex with different superscript numbers within a column differ at 0.05 level (Tukey's HSD test).

	Season			
	Spring	Summer	Autumn	Winter
M. ochrogaster				
Alfalfa				
Males	11.5 ± 0.8^{a1}	14.8 ± 0.6^{b1}	12.4 ± 0.5^{a1}	6.1 ± 0.4^{d1}
Females	6.3 ± 0.6^{ab1}	6.5 ± 0.4^{ab1}	7.2 ± 0.3^{a1}	6.2 ± 0.4^{b1}
Bluegrass				
Males	13.6 ± 0.9^{a2}	19.9 ± 1.2^{b2}	15.9 ± 0.9^{a2}	10.8 ± 0.6^{c2}
Females	9.9 ± 0.7^{a2}	11.6 ± 1.1^{a2}	9.9 ± 0.5^{a2}	9.3 ± 0.5^{a2}

Table 2 (Cont.)

Tallgrass				
Males	16.0 ± 1.0^{a2}	15.5 ± 1.1^{a2}	15.1 ± 1.0^{a2}	13.0 ± 0.8
Females	10.7± 0.9^{a2}	11.0 ± 0.8^{a2}	11.2 ± 0.8^{a2}	11.4 ± 1.0
Males; *F*, df	15.164, 2,974	4.186, 2,1101	16.797, 2,1865	51.270, 2,1
P	< 0.001	0.015	< 0.001	< 0.001
Females; *F*, df	16.435, 2,820	22.717, 2,1203	35.571, 2,2204	25.788, 2,1
P	< 0.001	< 0.001	< 0.001	< 0.001
M. pennsylvanicus				
Alfalfa				
Males	22.6 ± 2.5^{a1}	19.4 ± 2.4^{a1}	21.6 ± 2.1^{a1}	9.6 ± 1.5^{b1}
Females	17.0 ± 2.6^{a12}	11.5 ± 1.7^{ab1}	11.4 ± 1.1^{ab1}	7.6 ± 1.1^{b}

Table 2 (Cont.)

Bluegrass				
Males	19.8 ± 1.0^{a1}	18.3 ± 1.3^{a1}	18.3 ± 1.3^{a1}	14.2 ± 2.0^{b}
Females	12.4 ± 0.8^{a1}	11.8 ± 1.1^{a1}	12.9 ± 0.8^{a1}	12.5 ± 1.3^{a}
Tallgrass				
Males	18.6 ± 0.9^{a1}	22.5 ± 1.5^{b1}	30.1 ± 2.2^{b2}	18.0 ± 1.3^{a}
Females	13.2 ± 0.7^{a2}	13.3 ± 1.1^{a1}	16.2 ± 1.0^{a2}	15.2 ± 1.2^{a}
Males; *F*, df	1.383, 2,614	3.698, 2,315	6.924, 2,398	7.024, 2,3(
P	0.252	0.026	0.001	0.001
Females; *F*, df	3.573, 2,486	1.496, 2,270	8.106, 2,595	6.147, 2,3
P	0.029	0.226	< 0.001	0.002

Table 3. Home range indices (mean ± SE, in meters) in relation to population densities. Values of *F*-statistic, degrees of freedom and observed significance level (*P*) for one-way ANOVA comparing home range indices among the population density categories. Values within a row with different superscripts differ significantly at 0.05 level.

	Population density				F; df
	1-25/ha	26-50/ha	51-100/ha	≥101/ha	
M. ochrogaster					
Alfalfa					
Males	17.2 ± 1.1[a]	14.7 ± 1.3[a]	13.2 ± 0.6[a]	8.0 ± 0.4[b]	71.788; 3,
Females	8.6 ± 0.8[a]	8.3 ± 0.9[a]	7.4 ± 0.4[a]	5.6 ± 0.2[b]	45.573; 3,
Bluegrass					
Males	14.4 ± 0.7[a]	15.6 ± 0.8[a]	16.0 ± 1.0[a]	11.2 ± 0.7[b]	10.053; 3,
Females	10.5 ± 0.7[a]	11.9 ± 0.9[a]	10.6 ± 0.6[a]	7.5 ± 0.4[b]	10.599; 3,

Table 3 (Cont.)

Tallgrass					
Males	18.7 ± 1.2[a]	14.8 ± 1.1[a]	16.6 ± 1.1[a]	10.4 ± 0.7[b]	10.914; 3
Females	13.6 ± 1.0[a]	11.6 ± 1.2[a]	12.0 ± 0.9[a]	8.7 ± 0.7[b]	7.980; 3,
M. pennsylvanicus					
Alfalfa					
Males	17.5 ± 22.4[a]	26.0 ± 3.8[a]	17.8 ± 2.0[a]	21.7 ± 2.3[a]	1.971; 3,
Females	12.7 ± 2.3[a]	13.1 ± 2.5[a]	11.7 ± 1.1[a]	11.1 ± 1.5[a]	0.615; 3,

Table 3 (Cont.)

Bluegrass					
Males	21.6 ± 1.9[a]	24.3 ± 2.2[a]	18.4 ± 0.9[a]	15.0 ± 0.9[b]	5.982; 3,
Females	14.8 ± 1.5[a]	14.9 ± 1.4[a]	11.4 ± 0.6[b]	10.6 ± 0.8[b]	4.511; 3,
Tallgrass					
Males	28.7 ± 2.0[a]	20.5 ± 0.9[b]	13.6 ± 0.6[c]	14.5 ± 0.9[c]	215.086; 3
Females	16.8 ± 2.0[a]	14.9 ± 0.6[a]	11.0 ± 0.6[b]	9.1 ± 0.6[b]	17.083; 3

Table 4. Home range indices (mean ± SE, in meters) in supplementally fed and control sites. Values of *t* statistic, degrees of freedom and observed significance level (*P*) are given.

	Study site		*t*; df	P
	Supplementally fed	Control		
M. ochrogaster				
Bluegrass				
Males	18.4 ± 2.0	14.0 ± 1.1	1.27, 235	0.207
Females	9.0 ± 1.7	9.9 ± 0.9	1.46, 189	0.146
Tallgrass				
Males	14.0 ± 1.3	18.7 ± 2.0	1.74, 281	0.096
Females	11.4 ± 1.0	12.9 ± 2.0	0.303; 173	0.763
M. pennsylvanicus				
Bluegrass				
Males	17.7 ± 1.4	15.9 ± 0.9	1.33, 341	0.183
Females	11.2 ± 1.3	9.9 ± 0.5	0.28, 356	0.782
Tallgrass				
Males	13.2 ± 0.6	16.4 ± 0.7	3.17, 566	0.002
Females	10.2 ± 0.5	12.6 ± 0.6	3.32, 406.8	0.001