INFLUENCE OF POCKET GOPHERS ON MEADOW VOLES IN A TALLGRASS PRAIRIE

BENJAMIN A. KLAAS, BRENT J. DANIELSON, AND KIRK A. MOLONEY

Department of Animal Ecology, 124 Science II, Iowa State University, Ames, IA 50011 (BAK, BJD)
Department of Botany, Iowa State University, Ames, IA 50011 (BAK, KAM)
Present address of BAK: 1117A East Cota, Santa Barbara, CA 93103

Creation of mounds by plains pocket gophers (*Geomys bursarius*) may affect the distribution of meadow voles (*Microtus pennsylvanicus*) and subsequent patterns of herbivory. An association between abundance of meadow voles and density of neighborhood mounds might be expected if voles use mounds as feeding sites (positive association), or if vole avoid mounds due to lack of cover (negative association). Mounds also may indirectly affect vegetative patterns, if mounds affect the distribution of herbivores. During two consecutive summers, we livetrap vole and mapped mounds on three 80 m x 80 m plots. Regressions of vole captures at each trap station against the number of mounds within a range of ranges of each trap were consistently negative across most spatial scales, but strong-est correlation was found to be at 10 m. In all cases, bivariate scattergrams revealed a “factor-ceiling” distribution, with data points widely scattered below an upper limit. We also conducted an experiment to determine if seedlings had a greater or lesser mortality due to small-mammal herbivory when growing on mounds versus off mounds. A two-tailed paired t-test on the proportion of seedlings eaten after 13 days failed to show differences between on-mound and off-mound rates of herbivory ($P = 0.066$); however, prior analyses showing voles avoiding areas with high rates of disturbance give weight to the hypothesis that seedlings growing off mounds experience higher rates of herbivory. Thus, through a second-order indirect effect, the presence of gopher mounds could lead to distinct changes in the plant community.

Key words: *Geomys bursarius*, *Microtus pennsylvanicus*, disturbance, gopher mounds, microtine, indirect effects, seedling survival, tallgrass prairie

Fossorial rodents occur on all continents except Australia and Antarctica (Andersen, 1987) and have been shown to have dramatic impacts on plant communities (Andersen, 1987; Huntly and Inouye, 1988; Reichman and Jarvis, 1989). In North America, all below-ground herbivorous mammals are from the family Geomyidae (Nowak, 1991). They create extensive burrow systems that serve for both foraging and all other day-to-day activities. They are solitary and actively defend their burrows from conspecifics (Hansen and Miller, 1959).

Pocket gophers have been recognized as important agents of soil movement (Grinnell, 1923; Mielke, 1977), and soil from construction and maintenance of burrow systems is expelled periodically to the surface, creating a mound. These small patches of bare soil create microhabitats that differ from undisturbed soil in plant species composition and biomass (Hobbs and Mooney, 1985; Grant et al., 1980; Martens et al., 1990; Moloney and Levin, 1996; cf. Williams and Cameron, 1986). They also differ in soil chemistry (Grant and McBrayer, 1981; Reichman et al., 1993; Zinnel and Tester, 1990), and mounds are even known to be positively correlated with the presence of some species of grasshoppers (Huntly and Inouye, 1988).

Gophers are known to directly affect the plant community in tallgrass prairies...
(Brotherson, 1982; Gibson, 1989; Huntly and Inouye, 1988; Huntly and Reichman, 1994; Reichman, 1988; Reichman et al., 1993; Reichman and Smith, 1985; Tilman, 1983; Williams et al., 1986). In fact, Huntly and Inouye (1988:792) state that the effects of gopher mounds “cascade through the entire trophic web.” This may be especially true in tallgrass prairies where perennial grasses may limit availability of sunlight. Low-light levels at the soil surface may inhibit establishment of dicots (Hartnett and Keeler, 1995; Martinsen et al., 1990). Breaks in the prairie canopy caused by gopher mounds may counteract this effect and provide recruitment sites for seedlings. This, in turn, may result in a greater diversity of plants (Martinsen et al., 1990; Williams and Cameron, 1986; Williams et al., 1986). However, if mounds act as recruitment sites for seedlings, it follows that herbivores, which favor seedlings as forage, could be found in higher abundance in areas of high disturbance. Conversely, breaks in the prairie canopy might be avoided if they expose herbivores to predators (Batzi and Lesieutre, 1995; Getz et al., 1987; Jekanoski and Kaufman, 1995; Kotler et al., 1988).

Only one previous study has examined the influence of gophers on distribution of another mammalian herbivore common to tallgrass prairies. Whittaker et al. (1991) reported that adult male meadow voles (Microtus pennsylvanicus) showed a positive relationship with mounds and that voles, in general, crossed gopher mounds more than would be expected if they moved at random. However, reasons for such a relationship are unknown.

We tested two hypotheses. First, we hypothesized that distributions of mounds and the most abundant mammalian herbivore in our area, the meadow vole, would be strongly correlated. Second, we hypothesized that gopher activity would indirectly affect rates of herbivory on seedlings.

**METHODS**

**Study site and field methods.**—The study was conducted at Anderson Prairie, an 81-ha preserve in Emmet Co., NW Iowa, 3.5 km NW of the town of Estherville. The study area had a moderately diverse (ca. 160 plant species) black-soil tallgrass prairie with native (e.g., Andropogon gerardii, Sorghastrum nutans) and exotic (e.g., Bromus inermis, Poa pratensis) grass species in abundance. In May 1994, we staked out three 80-m by 80-m study plots, separated by ≥100 m each. We put permanent stakes at 10 m intervals throughout plots, creating three plots of 64 10-m by 10-m cells. These three plots (hereafter referred to as the N, SE, and SW plots) comprised a long-term study of spatial relationships of gopher mounds, small mammals, and vegetation patterns.

**Surveys of gopher mounds.**—On 23 May 1994, we counted all extant gopher mounds in each 10- by 10-m cell of the three plots. At ca. 1-week intervals thereafter, we located all new gopher mounds within the three plots and marked them with small plastic garden stakes. We recorded number of fresh mounds in each cell of the plots during each survey. Thus, for any cell within a plot during any given time period, the number of newly created gopher mounds was determined. On the N plot, we used a surveying transit to map locations of all gopher mounds and trap locations. With a relatively high degree of accuracy, we were able to obtain the location and timing (within ca. 1 week) of all gopher mounds created between 23 May 1994 and 3 August 1995 on the N plot. On the SE and SW plots, only weekly counts of mounds for each cell were recorded.

**Censuses of small mammals.**—From the initial counts of mounds on 23 May 1994, we categorized each 10- by 10-m cell in each study plot by its level of disturbance. Cells were assigned to categories of zero, low (1–2 mounds), medium (5–7 mounds), or high (>10 mounds) disturbance (gaps between categories ensured a wide range of distinctly different levels of disturbance; some cells fell in between categories, but 87.5% were contained in the four categories). In each plot, five cells from each category were chosen randomly as trapping cells. Within a trapping cell, five Sherman live traps were placed in fixed locations for the duration of the study (Fig. 1).

We livetrapped rodents for 3 consecutive days each week from 31 May to 11 August 1994 and from 9 May to 3 August 1995. The 100 Sherman live traps on each plot were opened on Monday,
Fig. 1.—Live-trapping design for meadow voles for the N (North) plot on Anderson Prairie. Each shaded 10- by 10-m cell had five Sherman live traps equally spaced in the arrangement shown above. Five cells were chosen randomly for trapping from each of four classes of initial densities of gopher mounds. Blank cells were surveyed for mound building but not for vole activity. The distribution of blank cells does not imply anything about the distribution of mounds. The SE (Southeast) and SW (Southwest) plots were trapped in a similar manner. Traps were run for 3 consecutive days each week for 11 weeks in 1994 and 14 weeks in 1995.

Tuesday, and Wednesday evenings at ca. 1700 h. Traps were baited with a small handful of dry oats. We checked traps the next mornings beginning at ca. 0700 h. Captured animals were identified, weighed, sexed, ear-tagged, and released. Thus, for any given trap during any given time period, counts of numbers of individuals and captures were obtained.

Seedling herbivory experiment.—We assessed the impact that germination site (on- versus off-mound) had on herbivory rates of seedlings using garden peas transplanted to the N plot in 1995. On 4 July 1995, we planted and germinated in a greenhouse 450 Wando variety garden pea seeds in #9 Jiffy peat pellets. Seeds were watered every day until germination, and then every other day for 14 days. After 14 days when the seedlings had reached an average height of ca. 50 mm, they were transplanted to the N plot. The experiment was conducted on this plot because it was the most mesic of the three plots, thereby maximizing transplanting success. This plot also had the highest amount of gopher activity.

For this experiment 37 mounds were selected randomly from a pool of gopher mounds created during the previous 3 weeks. We planted a cluster of nine pea seedlings (3 by 3 arrangement) in a square array ca. 10 cm on a side. We replaced the soil, leaving the mound appearing as before except for the nine seedlings growing in its center. On 12 mounds, we placed small (250 mm diameter, 250 mm tall) cylindrical enclosures of 6.4-mm mesh hardware cloth over seedlings, pushing enclosures 30–50 mm into the soil to secure them. Those enclosures prevented voles from eating seedlings. Over another 12 mounds, we placed enclosures similar to the first set but with three 100- by 100-mm openings ("doors") at equal intervals along the base. Those enclosures allowed voles access to seedlings but controlled for other unknown effects that enclosures may have on seedling survival.

The remaining 13 mounds were used for paired on-mound versus off-mound treatments. Each off-mound treatment was located 1 m west of the on-mound treatment. After parting the litter layer away from the area desired for planting, nine seedlings were placed in a 3 by 3 arrangement identical to other treatments. After planting, we repositioned litter and surrounding vegetation to mimic an undisturbed germination. Seedlings in all treatments were watered after
planting. Sufficient rains during the following 2 weeks made further watering unnecessary.

All treatments were checked for evidence of small mammal herbivory at 5 and 13 days after planting. We noted seedlings for their status (alive or dead), herbivory by insects (holes chewed in leaves), small mammals (stems clipped off at an angle), or none. After day 13, we removed all of the seedlings and exclosures from the study plot.

Data analysis.—To determine how local disturbances such as gopher mounds affect vole activity, it was necessary to define the term “local” explicitly. Arbitrarily imposing a single scale of observation may miss significant interactions at other scales of space or time (Levin, 1992). Therefore, we explicitly looked across a range of spatial and temporal scales and objectively determined the most appropriate spatial scale. That scale is referred to as the “neighborhood” when describing the relationship between voles and mounds. After proper spatial and temporal scales were identified, we examined data to identify consistent trends in relationships between densities of voles and mounds. That information was then coupled with the experiment on the herbivory of seedlings.

We used the high-resolution mound data taken with surveying equipment from the N plot to determine spatial and temporal scales at which gopher mounds most strongly influenced abundance of voles. We counted the number of mounds produced in a specified time (e.g., mounds created in 1994) and within given distances of each trap station. Those distances comprised a range of radii, r, from each trap location. Occasionally, those circles did not fall totally within the plot. In those cases, the following edge correction was used to adjust for low counts from missing data:

\[ C_{ec} = \frac{1}{b} C \]  

where \( C_{ec} \) was the edge-corrected count, \( b \) was the proportion of the circle contained within the study plot, and \( C \) is the uncorrected count from the mound data.

We obtained mound counts at 10 different radii (2.5 to 25.0 m in 2.5-m increments around each trap location) for four sets of temporally categorized mound data: all mounds, mounds from June 1994, mounds from June–September 1994, and mounds from March–June 1995. We calculated a series of 40 nonparametric rank regressions (Conover, 1980) with number of vole captures at each trap location as the dependent variable and number of mounds within the given radius of the trap as the independent variable. Data containing all mounds, “all mounds,” were used as an estimate of the general-spatial-disturbance rate (i.e., local probability of disturbance), and compared to 1994 and 1995 tallies of vole captures. The three remaining sets of mound counts were compared with tallies of vole captures only when the mound data preceded vole data. Thus, vole captures from 1994 were not compared with 1995 mounds, because voles from 1994 could not be dependent on mounds that had yet to be created. We plotted correlations of those regressions across the range of radii to determine the search radius with the highest descriptive power. This radius was called the “neighborhood” and was used for all subsequent comparisons of mound disturbance and vole abundance.

In exploring the temporal-scale issue, we divided mounds from 1994 and 1995 into two groups each: mounds from June 1994, mounds from July–August 1994, mounds from March–May 1995, and mounds from June 1995. Four nonparametric rank regressions (Conover, 1980) were compared using numbers of vole captures at each trap in 1995 as the dependent variable and number of mounds within the radius of the neighborhood (10-m radius) of each trap as the independent variable. From those comparisons, we determined the most descriptive temporal scale, and it was used in all further analyses.

On the SE and SW plots, we only had counts of the number of mounds within the 10-m by 10-m cells (not precise locations within each cell). Thus, we used the neighborhood radius (10 m) from the previous analyses of the N-plot with a technique for estimating counts of gopher mounds within the neighborhood of the trap (a circle of radius, r, from each trap location). Count estimates, \( C \), were determined by the equation:

\[ C = \sum_{i=1}^{n} p_i c_i \]  

where \( n \) was the number of cells contained within the circular neighborhood of the trap, \( p_i \) was the proportion of the area of the circle contained in cell \( i \), and \( c_i \) was the number of mounds in
cell i. When a circle was not wholly contained within a study plot, an edge correction was needed:

$$C_{ce} = \frac{1}{b} \sum_{i=1}^{b} p_i c_i$$ (3)

where $C_{ce}$ was the edge-corrected mound count and $b$ was the proportion of the circle contained within the study plot.

Using mound counts from this procedure, we ran nonparametric rank regressions (Conover, 1980) for vole captures in 1994 and 1995 at the temporal scale determined from the analyses of the N plot. To establish that the weighted-average technique was an adequate estimate of neighborhood disturbance rates, we applied the technique to the N-plot data and compared count estimates to those generated from the mound-search program. We then compared rank regressions from all three plots to look for a consistent relationship of voles to gopher mounds.

Density of local mounds, by itself, may not dictate mean activity of meadow voles at a given location. However, mound density may influence one or more extremes in vole activity. This type of relationship is common in ecological field data (Blackburn et al., 1992; Kaiser et al., 1994; Thomsen et al., 1996). For example, Thomsen et al. (1996) found that gopher activity affects the maximum number of flowers at a given location. At high levels of gopher activity, density of flowers can range only from none to very low. At locations with lower gopher activity, the maximum number of flowers that is observed at a given location increases, although the minimum number is still zero. Thomsen et al. (1996) referred to those types of patterns as “factor ceiling” distributions, with the independent variable placing a cap on values of the dependent variable. We have adapted a method from Blackburn et al. (1992) to evaluate our data with those ideas in mind. In this approach, regressions were performed on only the upper percentiles of the data (voles captures per trap) in discrete intervals of the independent variable (mound density), thereby fitting a least-squares line to the upper bound of the data distribution. For a given comparison of voles versus mounds, we divided the independent variable (mound density) into $k$ equal intervals according to the equation:

$$k = \frac{2n(100 - p)}{100}$$ (4)

where $n$ was the sample size and $p$ was the desired percentile to examine. In this case, we wanted to look at upper limits of vole activity, so we used the 95% level; therefore, $k = 10$ intervals in these regressions. For each interval, we plotted maximum number of vole captures, and we performed a simple linear regression. Factor-ceiling regressions were done for the three plots at the spatio-temporal scales identified by analyses of the N plot described above. We examined factor-ceiling regressions for consistent trends.

In analyzing the experiment on the herbivory of seedlings, data were tallied as the proportion of each replicate eaten by small mammals. Because of small samples, zeroes in the data were given the value of $1/4n$, and ones (100% mammal herbivory) were given the value of $(n - 1/4)/n$ (where $n = 9$, the number of seedlings within each replicate) following the suggestion of Snedecor and Cochran (1980). Values were arcsin square-root transformed to normalize data (Snedecor and Cochran, 1980). Transformed values for exclosures with doors were tested with a one-tailed $t$-test to see if they differed significantly from zero. We performed a two-tailed paired $t$-test on the rates of mean herbivory for the transformed on-mound and off-mound data.

RESULTS

Effects of gopher mounds on voles.—In 1994, 260 voles (1,043 captures) were captured, and in 1995, 161 voles (739 captures) were captured. The N plot had the highest number of individuals and captures in 1994 and the most individuals in 1995 (Table 1). Seven-hundred-eighty mounds were counted in 1994 and 1,261 in 1995. The N plot had the highest numbers of mounds in both years, followed by the SE plot and the SW plot (Table 1). There was a great deal of variation within plots; the number of mounds within a 10-m by 10-m cell ranged from 0 to 32 in 1994 and zero to 44 in 1995. The number of vole captures at a trap location varied from zero to 26 in 1994 and zero to 12 in 1995.

One cell in the N plot contained a disproportionately high number of vole captures (92 captures in 1994 and 25 captures
Table 1.—Summary statistics of meadow vole capture and individual live-trapping data and gopher mound surveys from 1994 and 1995. Individual totals were estimated from tallying unique ear-tag numbers in the data set. Retagged individuals were not counted in this total.

<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>490</td>
<td>119</td>
<td>301</td>
<td>68</td>
<td>432</td>
<td>650</td>
</tr>
<tr>
<td>SE</td>
<td>324</td>
<td>67</td>
<td>324</td>
<td>61</td>
<td>182</td>
<td>392</td>
</tr>
<tr>
<td>SW</td>
<td>229</td>
<td>74</td>
<td>114</td>
<td>32</td>
<td>166</td>
<td>219</td>
</tr>
<tr>
<td>Total</td>
<td>1,043</td>
<td>260</td>
<td>739</td>
<td>161</td>
<td>780</td>
<td>1,261</td>
</tr>
</tbody>
</table>

in 1995 versus an average number of captures in other N-plot cells of 20.95 and 14.53, respectively). That cell was distinctly different in vegetation and soil moisture and lower in relative elevation than and other cells. Because of extremes in vole abundance and environmental factors, capture data of voles from that cell were omitted in all analyses.

All slope estimates were negative for nonparametric rank regressions of vole captures on the numbers of gopher mounds across the 10 neighborhood radii on the N plot. Squared correlation values ranged from 0.001 (voles in 1995 versus mounds in 1995 at 25 m) to 0.261 (voles in 1995 versus mounds in 1994 at 10 m). In the four sets of regressions, a 10-m radius was consistently the most descriptive, with the exception of voles in July–August 1994 versus mounds in June 1994 (Fig. 2), where 15 m had a slightly higher correlation. Thus, a neighborhood radius of 10 m was used in all subsequent analyses.

In using the weighted-average technique (equation 3) for estimating mound densities in the 10-m neighborhoods around each trap station, the N-plot regressions produced correlations that were very similar to regressions that used data obtained by precisely surveying locations of individual mounds (Table 2). Thus, that technique was used to analyze data from the SE and SW plots. Like the N plot, all regressions for the SE plot were negative (Table 2). However, regressions with the highest correlations were voles in 1995 versus mounds in 1995 and voles in 1995 versus all mounds (both $r^2 = 0.232$), rather than voles in 1995 versus mounds in 1994 as in the N plot.

Of the four rank-regression slopes calculated for the SW plot, two were not significantly different from zero, one was positive, and one was negative (Table 2). We examined scatter plots of the raw (unranked) data from all three plots of voles in 1995 versus mounds in 1995 (Fig. 3) to determine the cause. From visual inspection, the SW plot, which produced a positive regression slope, looked similar to other plots. Upon closer inspection, however, we found that 15 of 100 points in Fig. 3 were null values for vole captures and mound counts. Those 15 points pulled the left end of the regression line down and created a
Table 2.—Correlation values for nonparametric rank regressions on four sets of comparisons of voles versus mounds. Direction of the slope for each regression is given if the slope is different from zero ($P < 0.05$). One cell from the N plot (5 of 100 points) was left out of the analyses as an outlier. For the N plot, the first column shows results of regressing ranks of vole captures against the number of mounds in a 10-m search radius using mapped mound locations. The second column used the weighted-average technique, which was also used for the SE and SW plots.

<table>
<thead>
<tr>
<th>Regression (voles versus mounds)</th>
<th>N plot (surveyed data)</th>
<th>N plot (weighted-average)</th>
<th>SE plot (weighted-average)</th>
<th>SW plot (weighted-average)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sign of slope</td>
<td>$r^2$</td>
<td>Sign of slope</td>
<td>$r^2$</td>
</tr>
<tr>
<td>1995 versus 1994</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995 versus 1995</td>
<td>$-$</td>
<td>0.261</td>
<td>$-$</td>
<td>0.232</td>
</tr>
<tr>
<td>1995 versus all</td>
<td>$-$</td>
<td>0.124</td>
<td>$-$</td>
<td>0.11</td>
</tr>
<tr>
<td>1994 versus June</td>
<td>$-$</td>
<td>0.208</td>
<td>$-$</td>
<td>0.168</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td>0.128</td>
<td>$-$</td>
<td>0.092</td>
</tr>
</tbody>
</table>

After eliminating those null values, the regression resulted in a negative slope that did not differ from zero ($P = 0.43$). Thus, significantly negative slopes were observed for comparisons in the N and SE plots, but only one of the four slopes on the SW plot was significantly negative, although scatter plots of data appeared very similar.

Further visual inspection of scatterplots of mound densities and vole activity (Fig. 3) suggested that gopher activity may set maximal levels to vole activity but not minimal levels. In such cases, factor-ceiling regressions may be more appropriate than more conventional regression methods (Thomson et al., 1996). Such regressions were performed for all three plots comparing voles in 1995 to mounds in 1995, mounds in 1994, and all mounds and com-

![Scatter plots of vole capture at each trap station during July–August 1995 versus the numbers of mounds created within 10 m of each trap station during March–May 1995. Rank regressions of these data show a significant negative slope for the N and SE plots, but a significant positive slope for the SW plot. Note the different scale for mound densities on the N plot due to higher mound-building activity.](image)
Table 3.—Correlation values for 12 factor-ceiling regressions of voles versus mounds. One cell from the N plot was left out as an outlier (see text for explanation for factor-ceiling regressions). Slopes for all regressions were negative.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Comparison</th>
<th>$r^2$</th>
<th>$P$ (slope = 0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1994 June 1994</td>
<td>0.603</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>1995 1994</td>
<td>0.475</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>1995 1995</td>
<td>0.235</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>1995 All years</td>
<td>0.403</td>
<td>0.05</td>
</tr>
<tr>
<td>SE</td>
<td>1994 June 1994</td>
<td>0.290</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>1995 1994</td>
<td>0.395</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>1995 1995</td>
<td>0.483</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>1995 All years</td>
<td>0.393</td>
<td>0.05</td>
</tr>
<tr>
<td>SW</td>
<td>1994 June 1994</td>
<td>0.588</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>1995 1994</td>
<td>0.534</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>1995 1995</td>
<td>0.508</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>1995 All years</td>
<td>0.531</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Fig. 4.—Comparisons of regressions of numbers of gopher mounds within 10 m of each trap location and vole captures in 1995. Each bar represents a different set of mound data. Analyses using temporal scales of <1 year did not explain patterns of variation in the vole-mound relationship as well as scales of ≥1 year.

Thus, it appeared that the best predictor of vole activity was number of mounds created during the previous summer.

Effects of gopher mounds on herbivory.—No small-mammal herbivory was observed in the total-exclosure treatment. Of remaining treatments, frequency of mammalian herbivory was lowest for exclosures that had doors. That indicated that the hardware-cloth cages inhibited herbivory, although the average proportion of seedlings that were consumed totally was significantly greater than zero in this treatment ($P < 0.05$).

Seedlings classified as having experienced herbivory by small mammals were identical in appearance (leaves gone, stems chewed off at an angle) to plants near hay piles made by *M. pennsylvanicus* (B. A. Klaas, in litt.). Thus, we conclude that total exclosures were effective in excluding small-mammal herbivores, and that we successfully identified herbivory by small mammals.

Of the treatments without exclosures, seedlings in the on-mound treatment expe-
rienced less herbivory than seedlings in the off-mound treatment, as measured by either total number of seedlings eaten or average proportion of seedlings eaten per array. However, the observed difference in average proportion of seedlings eaten between on-mound and off-mound treatments was not significant (two-tailed paired t-test, $P = 0.066$).

**Discussion**

*Disturbance and herbivores.*—If physical factors, such as gopher mounds, influence habitat selection by voles, each vole must perceive its individual landscape at some particular spatial scale when judging local habitat quality. One reasonable estimate of such a scale might be the individual’s home range. Home-range size can be difficult to define (Burt, 1943; McNab, 1963), but the polygons describing daily activity patterns in *Microtus pennsylvanicus* given by Madison (1985) show areas similar in size to a circle with a 10-m radius. Bowers et al. (1996) also estimated home-range sizes for *M. pennsylvanicus* at different levels of habitat fragmentation. In contiguous habitat, estimates of the radius of an average of home range were 9.5 m for adult females and 10.5 m for adult males. It is, perhaps, not coincidental that the radius of a vole’s home range and the radius producing the strongest vole-mound correlation at a trap site (Fig. 2) are both ca. 10 m.

The factor-ceiling analysis is one of only a few that have been described explicitly in the ecological literature (Blackburn et al., 1992; Kaiser et al., 1994; Maller et al., 1983; Thomsen et al., 1996). Nonetheless, this type of relationship may be quite common, and we believe that conclusions from factor-ceiling regressions best describe of the observed patterns from the field. Unfortunately, factor-ceiling regressions do not provide much insight into factors that might regulate the dependent variable (in our case vole activity) below the ceiling. Thus, we can only speculate that it is probable that the lack of cover in areas of high mound density may set the upper limit to local vole activity, but other factors also must regulate vole activity much of the time.

*Microtus pennsylvanicus* has a host of avian and terrestrial predators (Pearson, 1985) and is known to have an affinity for habitat with a high percentage of cover (Zimmerman, 1965), presumably for protection. While voles consistently show negative relationships with gopher mounds at the scale of ca. 300 m², the plot with the most vole captures and individuals in 1994 and most individuals in 1995 had the most gopher mounds in both years, and the plot with the least vole captures and individuals in both years had the least mound activity in both years (Table 1). This suggests that at larger scales (ca. 6,400 m²) environmental factors may affect abundances of voles and gophers in the same manner, although at smaller scales (ca. 300 m²) there is a negative relationship.

Temporally, a vole’s perception of what a gopher mound represents may change as the mound ages and gradually becomes revegetated. The data suggest that voles are affected most strongly by mounds of ca. 1 year of age (Fig. 4). However, finer temporal scales of resolution (i.e., intervals < 1 year) that produce weaker correlations with vole activity may reflect social interactions between individuals that prohibit immediate spatial reshuffling in response to changes in habitat quality (e.g., mound density).

Significance of the negative correlation between gopher activity and the upper limits on vole activity may be important in structuring prairie plant communities if mound density indirectly affects seedling success, especially because all seedlings that were attacked were killed. After 5 days of our seedling experiment, only two seedlings had experienced herbivory by small mammals. However, by day 13, 139 of 342 (41%) seedlings available to voles had been attacked. Although we did not observe any significant environmental changes that may
have caused the increase between days 6–13, 92% of the seedling arrays that experienced herbivory encountered it first in this interval.

Survival of seedlings on mounds and off mounds did not differ, although lower survival of seedlings on mounds was consistent with the negative relationship observed between vole activity and gopher mounds. We believe that the large variation in vole activity in neighborhoods of low mound density (i.e., regions of low mound density do not necessarily have high vole activity) may explain why this difference was not more pronounced.

Because the majority of prairie plants are perennials and many of them reproduce clonally, recruitment from seed may not play a major factor in structuring prairie vegetation (Hartnett and Keeler, 1995). However, a recent study of species richness in tallgrass plant communities in Wisconsin (Leach and Givnish, 1996) documented that small fragments (0.2–0.6 ha) of native prairie have lost significant numbers of species over the last 32–52 years. Leach and Givnish (1996) suggest that lack of natural wildfires may be the cause of these extinctions, but if small fragments will not consistently support gopher activity, this also may contribute to the slow decline. It also is interesting that the plant species most commonly lost in these prairie fragments are legumes, which are highly desirable items in the diet of *M. pennsylvanicus* (Lindroth and Batzli, 1984). In any event, if the interaction between gophers and voles is maintained for long periods of time, it has the potential to affect vegetative patterns in the form of species abundances and community heterogeneity and perhaps promote high levels of plant species richness characteristic of tallgrass prairie ecosystems.

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