limestone breaks and uplands by *P. maniculatus* on KONZA (Finck et al., 1986) may affect the distribution of *P. leucopus* in the prairie. Use of unburned lowland stations by *P. leucopus* in the absence of *P. maniculatus* may result from competition between the two species. However, without experimental evidence of competition, the simplest explanation for our observations is differential habitat selection.

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**LITERATURE CITED**


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**HOME RANGE DYNAMICS AND ACTIVITY PATTERNS OF MICROTUS OCHR OGASTER AND SYNAP TOMYS COOPERI IN SYNTOPY**

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Prairie voles (*Microtus ochrogaster*) and southern bog lemmings (*Synaptomys cooperi*) commonly occur together in old field habitats (Gaines et al., 1977; Rose and Spevak, 1978). These small microtines are similar in size and morphology, and both species are herbivores which share common runway systems. Interspecific competition for food and/or space is likely under these circumstances (Grant, 1972). Based on paired encounters in the laboratory, Rose and Spevak (1978) concluded that prairie voles behaviorally dominated southern bog lemmings in a neutral arena. They did not consider the effect of site residency on behavioral interactions, even though residency status is an important determinant of dominance relationships in many mammals (e.g., Dobson, 1983; Trombulak, 1985; Wolff et al., 1988).

We used radio telemetry and supplemental live trapping to examine the influence of site residency and interspecific interactions on spatial and temporal patterns of habitat use in these two species. Specifically,
Fig. 1.—Solid lines represent the minimum convex polygon (CP) that encloses 90% of the locations for *M. ochrogaster*. The dotted lines indicate the same for *S. cooperi*. Right and left diagonal shading represents minimum 50% polygons for males and females respectively. Individuals without shading did not establish a home range as defined by any of the measures of home range establishment (see text). Open circles represent captures of resident *S. cooperi* for the trapping session immediately preceding the telemetry studies.

we looked at: (1) the abilities of nonresident voles and lemmings to establish home ranges in a resident population of *S. cooperi*; (2) the dispersion of successful colonizers in relation to conspecifics and heterospecifics; (3) diel activity patterns; and (4) microhabitat selection.

*Study area and sampling methods.*—The study was conducted in a 0.8 ha enclosure 10 km north of Lawrence in northeastern Kansas. The enclosure was constructed of 11 mm wire mesh fencing that extended 0.4 m below and 0.7 m above ground level. The enclosure did not inhibit movements of voles, based on a comparison of home range size with conspecifics on a nearby unenclosed area (cf., Swihart and Slade, 1984). Vegetation within the enclosure consisted primarily of brome grass (*Bromus inermis*), goldenrod (*Solidago* spp.), and compass plants (*Silphium perfoliatum*).

A 10 by 10 trapping grid was established inside the enclosure in September 1982. A single noncollapsible Sherman live trap was placed at each station, and adjacent stations were positioned 7.5 m apart. Trapping was conducted for two days at biweekly intervals, and all *M. ochrogaster* were removed from the enclosure before we initiated radio tracking. Resident lemmings were released at the capture site.
Four periods of radio tracking were conducted between trapping sessions: two in summer 1983, one in spring 1984, and one in summer 1984. Radio-tracked animals of both species were obtained from outside the enclosure to standardize, among individuals, the degree of familiarity with the enclosed habitat. Following abdominal implantation of the transmitters (Custom Electronics of Urbana Inc., weight <2.5 g, frequency range 150–151 MHz), individuals of both species were held in the lab for 24–48 h and then released into the enclosure. We waited an additional 12–18 h before beginning to track individuals to avoid recording any abnormal movements elicited by their release into a novel area (cf. Webster and Brooks, 1980). Telemetry sessions were 1.0 to 3.5 days in duration and were designed so that all portions of the circadian cycle were equally represented. If possible, each individual was located at 10-min intervals via triangulation. However, during the course of the study it was necessary to follow three animals on an hourly schedule to enable the 10 min sampling scheme to be maintained for the remaining individuals.

Within five days of the completion of a tracking period, habitat sampling was conducted along the longest axis of each animal’s home range. Five vegetation sample sets, each 3 m apart, were collected for each individual. For each set, forbs were counted in a 1 m² quadrat, and the density of graminoids was determined within a 0.01 m² quadrat. Collections of soil and grass samples were made in each quadrat to estimate moisture content. Litter depth was also measured at each sample site. To test for microhabitat selection (i.e., nonrandom use of habitat), identical sampling procedures were used with randomly placed transects (see Carnes and Slade, 1982).

**Home range establishment**.—As an objective means of determining whether nonresidents were establishing home ranges, we adopted Munger’s (1984) functional definition of a home range. He postulated that an individual occupied a true home range if it exhibited site fidelity, i.e., if the observed home range was significantly smaller than the mean home range size predicted under rules of random movement. We modified Munger’s simulation technique to quantify the level of site fidelity. For a given individual, we calculated the distance between successive observations. The order of these distances was randomized, and each distance was assigned a compass heading chosen randomly from the uniform interval (0°, 360°), thereby generating a sequence of movement vectors (cf. Munger, 1984). By using this randomized sequence of vectors, a utilization distribution was generated. This procedure was repeated 100 times, resulting in 100 random home ranges. For each random home range, three measures of home range size were computed: minimum convex polygon (CP; Jennrich and Turner, 1969); mean squared distance from the center of activity (MSD; Calhoun and Casby, 1958); and linearity ratio, the ratio of the distance between an individual’s first and last positions and the total distance moved (LR; Bell and Kramer, 1979). Each of these measures

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**Table 1.**—Observed home range measures and the probabilities (in parentheses) of their occurrence under the rules of random movement set forth in the text. M = male, F = female, CP = convex polygon, MSD = mean squared distance from the center of activity, LR = linearity ratio, Su = summer, Sp = spring. Periods are denoted by season and year of occurrence; a and b represent separate periods in summer 1983.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Period</th>
<th>CP</th>
<th>MSD</th>
<th>LR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microtus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>675F**</td>
<td>Su 83a</td>
<td>0.41 (0.01)</td>
<td>0.07 (0.02)</td>
<td>0.025 (0.60)</td>
</tr>
<tr>
<td>202F**</td>
<td>Su 83b</td>
<td>0.12 (0.02)</td>
<td>0.03 (0.01)</td>
<td>0.067 (0.14)</td>
</tr>
<tr>
<td>923M*</td>
<td>Su 83b</td>
<td>0.21 (0.01)</td>
<td>0.01 (0.01)</td>
<td>0.015 (0.04)</td>
</tr>
<tr>
<td>173M*</td>
<td>Sp 84</td>
<td>0.27 (0.01)</td>
<td>0.02 (0.01)</td>
<td>0.009 (0.06)</td>
</tr>
<tr>
<td>253F*</td>
<td>Sp 84</td>
<td>0.16 (0.01)</td>
<td>0.01 (0.01)</td>
<td>0.018 (0.04)</td>
</tr>
<tr>
<td>483F*</td>
<td>Sp 84</td>
<td>0.10 (0.01)</td>
<td>0.03 (0.01)</td>
<td>0.033 (0.06)</td>
</tr>
<tr>
<td>296M*</td>
<td>Su 84</td>
<td>0.22 (0.01)</td>
<td>0.02 (0.01)</td>
<td>0.008 (0.02)</td>
</tr>
<tr>
<td>346F*</td>
<td>Su 84</td>
<td>0.11 (0.02)</td>
<td>0.02 (0.01)</td>
<td>0.020 (0.06)</td>
</tr>
<tr>
<td>434M</td>
<td>Su 84</td>
<td>0.22 (0.70)</td>
<td>0.14 (0.94)</td>
<td>0.313 (0.93)</td>
</tr>
<tr>
<td>474M*</td>
<td>Su 84</td>
<td>0.20 (0.02)</td>
<td>0.02 (0.01)</td>
<td>0.033 (0.06)</td>
</tr>
<tr>
<td>Synaptomys</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>698F***</td>
<td>Su 83b</td>
<td>0.09 (0.01)</td>
<td>0.01 (0.01)</td>
<td>0.019 (0.17)</td>
</tr>
<tr>
<td>333M**</td>
<td>Sp 84</td>
<td>0.24 (0.01)</td>
<td>0.02 (0.01)</td>
<td>0.028 (0.38)</td>
</tr>
<tr>
<td>392F</td>
<td>Sp 84</td>
<td>0.60 (0.36)</td>
<td>0.13 (0.52)</td>
<td>0.052 (0.80)</td>
</tr>
<tr>
<td>311M</td>
<td>Su 84</td>
<td>0.67 (0.82)</td>
<td>0.12 (0.57)</td>
<td>0.059 (0.66)</td>
</tr>
</tbody>
</table>

* Indicates the animal successfully established a home range.
** These individuals shifted their centers of activity during the study. Other aspects of their movements were indistinguishable from successful colonizers.
characterizes space use differently. CP is a nonstatistical measure of dispersion of the total area used. MSD is a measure of dispersion of use around an arithmetic center, and LR measures shifts in the home range.

For each home range measure, the 100 values were ordered, thus forming an empirical sampling distribution with which the observed estimates could be compared. If all three values (CP, MSD, LR) from the observed data were smaller than the values for the tenth percentile of the randomized distributions, we considered the animal successful at establishing a home range. Otherwise, we concluded that the movements of the individual did not constitute a successful home range establishment. The decision to use the tenth percentile as our significance level was arbitrary. We chose a value greater than the fifth percentile in an attempt to balance trade-offs between type I and type II errors (Swihart and Slade, 1986; Toft and Shea, 1983). Using this method, seven of the ten voles established home ranges, but none of the four lemmings for which we had sufficient telemetry data did so (Table 1). Using LR as a measure of an animal’s tendency to shift its location over the study period, one vole (675F) and one lemming (333M) exhibited clear home range shifts. Vole 202F and lemming 698F exhibited slight shifts in their home ranges, but other aspects of their use of space were typical of successful colonizers (Table 1). Three individuals (434M, 311M, 392F) exhibited no site fidelity whatsoever as measured by CP, MSD, or LR (Table 1). Except for these three nomadic individuals, both species showed strong central tendencies in their utilization of space. Individuals spent most of their time in a core area near the center of their ranges (Fig. 1) and did not show indications of patrolling the periphery of their ranges.

Influence of residency status.—Although the majority of introduced voles successfully established home ranges, establishment usually did not occur in areas occupied by resident lemmings (Fig. 1). However, the density of lemmings in the spring of 1984 was low, thus overlap with residents was less likely than during the other periods. Only two voles (675F, 202F) exhibited prolonged activity in areas heavily used by resident lemmings, and one of these individuals eventually moved to an area of low lemming density (Fig. 1, Summer 83a). Because these individuals had high linearity ratios, neither vole was classified as successful in its attempt to establish a home range (Table 1).

Although southern bog lemmings have been characterized as subordinate to prairie voles in dyadic encounters in neutral arenas (Rose and Spevak, 1978), our results suggest that introduced voles did not displace resident lemmings. Hence, site residency was an important determinant of interspecific dominance. Although site-specific dominance relationships are common intraspecifically (e.g., Dobson, 1983; Trombulak, 1985; Wolff et al., 1983), they are not well known between species in natural microtine communities. Our findings contrast with earlier interspecific studies of similar-sized rodents which have shown that an aggressive species can invade a population of another species and eventually displace the original residents (e.g., Linzey, 1984; Myllymaki, 1977; Randall, 1978).

Interactions of introduced voles and lemmings.—Introduced lemmings avoided areas occupied by introduced voles. This was especially evident in the 1984 sessions when two lemmings that initially overlapped extensively with several voles shifted their locations to areas which were not being used by voles at that time (Fig. 1). Although one of the lemmings eventually settled within the home range of a vole, the vole was at the northern extreme of its range when the lemming arrived and there was no spatial overlap of the animals’ activities during the remainder of the session (Fig. 1, Summer 84). These results support Rose and Spevak’s (1978) conclusions: in a novel environment, prairie voles are dominant to lemmings, and lemmings are more likely to practice avoidance.

In our study, the following hierarchy was evident: lemmings were dominant to prairie voles when the former enjoyed the advantage of residency. However, when both species were attempting to secure new home ranges, voles were dominant. This hierarchy was supported by the data on home range establishment; presumably all resident lemmings occupied home ranges, most (but not all) introduced voles established home ranges, and none of the introduced lemmings succeeded in procuring a home range (Table 1).

Temporal activity patterns.—As a measure of activity patterns for each individual, we summed the distances traveled within 2 hours of time and divided that sum by the total distance traveled. These proportions were then averaged for each species during each season to produce a diel distribution of activity (Fig. 2).

Because voles and lemmings may share the same runways, subordinate individuals (introduced lemmings) may seek to reduce contacts with dominant animals (introduced voles and resident lemmings) by shifting their periods of activity (Glass and Slade, 1980). However, there was little evidence of temporal partitioning among radio-tracked individuals of the two species; both species exhibited primarily nocturnal behavior. This was not surprising given that the introduced lemmings shifted to areas not occupied by voles.

During the spring, lemmings became most active well after sunset, followed by 4 h of little movement and then another burst of activity at dawn, suggesting a bimodal distribution with fairly constant activity between peaks. Similar bimodal activity cycles have been noted for a variety of rodents (e.g., Kilduff and
Dube, 1979; Prochaska and Slade, 1981). This pattern shifted significantly during the summer to one of consistently low diurnal activity (0600 h to 1800 h, \( P < 0.02 \), sign test). The more constant nocturnal activity may have been a compensatory response to forced inactivity during the hot diurnal periods. Temperatures during the summer periods consistently climbed to 35°C or higher. Droughts also persisted in both summer periods, with little or no precipitation falling in the 3–4 weeks prior to each experimental period.

Although lemmings showed a pronounced seasonality in their activity patterns, voles modified their activity only slightly. Their diurnal activity was not noticeably depressed during summer. Even though summer conditions are severe enough to depress reproduction for this species (Gaines and Rose, 1976), its activity was affected less than that of lemmings by hot, dry weather.

Microhabitat selection.—Analysis of variance revealed no differences between the species with regard to habitat use (\( P > 0.05 \) for all variables examined). Southern bog lemmings have been associated with mesic habitat (Getz, 1961) and differences in vegetative associations have been demonstrated for S. cooperi and M. pennsylvanicus (Getz, 1961; Linzey, 1984). We believe the similarities in the vegetation of areas used by the lemmings and prairie voles in our study stem from the highly uniform nature of the old field habitat in which our study was conducted. Furthermore, in summer no mesic sites were available. Because we found no differences between the species, we pooled habitat data and compared it to data collected at randomly selected sites in the enclosure. The only detectable evidence of microhabitat selection was for...
drier sites in the spring when frequent rains caused occasional flooding. Radio-tagged animals chose regions with significantly lower soil moisture (soil moisture: home ranges = 16.5%; random samples = 22.4%; \( P = 0.04 \), \( t \) test). The regions may have had better drainage and hence, less chance of burrows being flooded.

Our data indicate that although the lemmings reduced diurnal activity to a greater degree than the voles during the summer, there was no evidence of temporal partitioning nor were there significant microhabitat differences, either of which could have resulted from interspecific competition. However, interspecific spatial partitioning did occur; nonresident voles avoided areas occupied by resident lemmings, and nonresident lemmings avoided areas containing nonresident voles. The motivating factor behind this avoidance behavior may have been competition for drier burrow sites during periods of high precipitation as indicated by our microhabitat analysis; however, we also found spatial partitioning during the summer when excess moisture was not a problem.

Although we could not monitor home range establishment in a resident population of prairie voles, such a study would be useful in determining the generality of our results. If site-specific dominance were operative, we would expect resident voles to dominate introduced voles and introduced lemmings to be subordinate to both classes of voles in terms of space use.

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