

Microhabitat Utilization and Species Distribution of Sympatric Small Mammals in Southwestern Ontario

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ABSTRACT: To examine predictable patterns of small mammal species distribution several habitat measures were taken, and small mammal species recorded, in six major habitat types in southwestern Ontario. *Peromyscus leucopus*, *P. maniculatus*, *Microtus pennsylvanicus*, *Tamias striatus*, *Zapus hudsonius* and *Blarina brevicauda* were captured in large enough numbers for multivariate analysis. All species pairs except *Blarina-Zapus* were found to be significantly different in habitat utilization due to a combination of tree basal area, amount of vegetation between 0.25 m and 1 m, number of trees, depth of dead grasses, leaves and other debris on the soil surface, and proportion of trees with first branches between 2 m and 3 m. Individual species predictably selected significantly different microhabitats.

Species density of small mammals in southwestern Ontario was significantly correlated with the depth of dead grasses, leaves and other debris on the soil surface, a probable indicator of runway suitability and available productivity. Mean foliage height diversity was correlated with species density, whereas most measures of horizontal habitat heterogeneity were not good predictors of species number.

INTRODUCTION

The scientific study of repeated patterns in species distribution is an important component of ecology. Ecologists need a strong empirical base from which to generate predictive syntheses of the utilization of space by animal species. Additionally, an understanding of factors responsible for species presence or absence in given habitats and relative abundances in these habitats is prerequisite to objective evaluation of the evolution of habitat selection.

One method in this search for repeated patterns is to evaluate the relative importance of factors that previously have been shown effective in predicting species distribution. Another approach is the evaluation of the effectiveness of a given factor or series of factors in determining the use of space within and among members of a locally co-occurring assemblage of species. I have used both of these in studies of sympatric small mammals in southwestern Ontario.

Geographically and regionally, we can often associate a given small mammal species with a particular gross habitat type. Thus, in middle North America, the white-footed mouse, *Peromyscus leucopus*, is associated with forested or bushy areas. Another form of habitat selection must occur locally because white-footed mice are not found in all wooded areas, or at all locations within these habitats. Individual *P. leucopus* as well as other small mammals must have a more refined form of subtle habitat selection. This is likely related to the structure of the environment, its productivity and/or the effect of the presence or absence of other similar species.

In studies of local populations of *Peromyscus leucopus* in Point Pelee National Park, M'Closkey and Lajoie (1975) showed that the density of these mice was significantly correlated with the density of vegetation less than 7.6 cm in height. *Peromyscus leucopus* density is associated with microhabitat structure. Further studies at Point Pelee using arboreal tracking techniques revealed that white-footed mice used local habitat patches in relation to their structural characteristics (diversity of branch angles and quantity of horizontal runways, M'Closkey, 1975a). These results were reconfirmed by similar track monitoring experiments of *P. leucopus* activity in man-made "bushes" (M'Closkey, 1976). M'Closkey (1975b) and M'Closkey and Fieldwick (1975) have also demonstrated that the distribution of the meadow vole

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(*Microtus pennsylvanicus*) can be predicted from knowledge of microhabitat structure.

Since it appears that the distribution of selected small mammals is a repeated function of structural habitat characteristics, I reasoned that the use of space of all species in a local small mammal fauna should be predictable through quantitative analysis of microhabitat. Furthermore, I postulated that along with other biological dissimilarities, different species distributions should be predictable on the basis of differential species-wise importances of microhabitat characteristics. Certain microhabitat characters, however, are likely important in the selection of habitat by small mammals in general. If this latter point is true, then as these characters increase in quantity, more species should co-occur in localized environments.

In southwestern Ontario commonly captured rodents include [common names and minimum-maximum adult body weights from Burt (1948) and Peterson (1966) in parentheses]: three cricetids, the cricetines, *Peromyscus leucopus noveboracensis* (white-footed mouse, 12-31 g), a woodland resident; *P. maniculatus bairdii* (prairie deer mouse, 10-24 g), a grassland species; and the microtine, *Microtus pennsylvanicus* (meadow vole, 20-68.6 g), in similar habitats to, and frequently microsympatric with *P. maniculatus bairdii*; a sciurid, *Tamias striatus* (eastern chipmunk, 66-115 g), a woodland species; and a zopodid, *Zapus hudsonius* (meadow jumping mouse, 10-22.5 g) another grassland species. In addition, an insectivore, *Blarina brevicauda* (short-tailed shrew, 12-27 g), is prevalent and often captured in habitats ranging from dense grasses to mature forest.

STUDY AREAS AND SPECIES OF SMALL MAMMALS

From May through October 1975 fieldwork was conducted in a 5-ha mature forest isolated by surrounding farmland, and in an 81-ha wet prairie in the Windsor Prairie Provincial Nature Reserve, Essex County, southwestern Ontario. The forest consisted of silver and hard maple (*Acer saccharinum*, *A. saccharum*), white ash (*Fraxinus americana*), basswood (*Tilia americana*), blue beech (*Carpinus carolinia*), both red and white oak (*Quercus* spp.), several species of elm (*Ulmus*) and hickory (*Carya*), with a small number of sycamore (*Platanus occidentalis*), beech (*Fagus grandifolia*) and hawthorn (*Crataegus* spp.). Understory vegetation was mostly young trees, riverbank grape (*Vitis riparia*), brambles (*Rubus* spp.), a few small chokecherry (*Prunus virginiana*) and prickly ash (*Zanthoxylum americanum*). Ground cover was seasonal with spring flowers, including jack-in-the-pulpit (*Arisaema triphyllum*), wild geranium (*Geranium* sp.) and trillium (*Trillium* sp.), becoming subordinate in summer to dense stands of poison ivy (*Rhus radicans*). In addition, most large trees were draped with vines of one or more of grape, poison ivy and Virginia creeper (*Parthenocissus vitacea*). *Peromyscus leucopus*, *Zapus hudsonius*, and *Blarina brevicauda* were captured in this mature forest habitat (Table 1).

The prairie has been described by M'Closkey and Fieldwick (1975), and contains five species of small mammals: *Peromyscus leucopus*, *Microtus pennsylvanicus*, *Tamias striatus*, *Zapus hudsonius* and *Blarina brevicauda* (Table 1).

Because of the low numbers of *Microtus* captured and also to obtain habitat data on closely related species (congeners), I censused two agricultural areas where both *Microtus* and *Peromyscus maniculatus* were known to co-occur: (1) a 20.3-ha hayfield composed primarily of alfalfa (*Medicago sativa*), red clover (*Trifolium pratense*) and timothy (*Phleum pratense*); (2) an 8.1-ha field of wheat stubble (*Triticum aestivum*) containing foxtail (*Setaria* sp.) and ragweed (*Ambrosia* sp.). Two small old-fields (0.54 and 1.22 ha) dominated by mixed grasses and goldenrod (*Solidago* spp.) also were monitored.

TABLE 1.—Sampling effort (trap nights), number of captures of small mammals and small mammal species density in several habitats in southwestern Ontario. Animals are assumed to be residents where captured, though for species with small sample sizes, residency cannot be empirically determined for all habitats. See text for detailed habitat descriptions

| Habitat | Trap nights | <i>Peromyscus leucopus</i> | <i>Peromyscus maniculatus</i> | <i>Tamias striatus</i> | <i>Microtus pennsylvanicus</i> | <i>Zapus hudsonius</i> | <i>Blarina brevicauda</i> | Species density |
|---------------------|-------------|----------------------------|-------------------------------|------------------------|--------------------------------|------------------------|---------------------------|-----------------|
| Hay | 75 | 0 | 15 | 0 | 2 | 0 | 0 | 2 |
| Stubble | 73 | 0 | 9 | 0 | 1 | 0 | 0 | 2 |
| Old field (0.54 ha) | 36 | 0 | 1 | 0 | 2 | 0 | 0 | 2* |
| Old field (1.22 ha) | 50 | 3 | 1 | 0 | 1 | 0 | 0 | 3* |
| Mature forest | 1270 | 219 | 0 | 0 | 0 | 3 | 2 | 3 |
| WET PRAIRIE | | | | | | | .. | .. |
| Old field | 1300 | 29 | 0 | 0 | 4 | 7 | 0 | 3 |
| Open woods | 1250 | 93 | 0 | 9 | 0 | 0 | 1 | 3 |
| Savanna | 1050 | 54 | 0 | 10 | 2 | 4 | 5 | 5 |
| Total | 5104 | 398 | 26 | 19 | 12 | 14 | 8 | .. |

* Too few capture points to be used in regression analysis of habitat heterogeneity versus small mammal species density

METHODS

In the wet prairie, three 10×10 trap grids with 15-m spacings were abutted to one another, giving an enclosed trap area of 5.87 ha. These were arranged so that grids I (old-field, composed of short grasses and herbs, with a few invading shrubs) and II (open woods, with medium-sized oak trees having a discontinuous canopy and a vegetation layer of ferns) were separated by a sharp ecotone between the two habitats. Grid III (savanna) was similar to the open woods, but included many open grassy habitats.

In the mature forest, I also constructed a 10×10 grid. To look at a possible edge effect of the forest on small mammal density, I added two more rows of trap stations. The result was a 10×12 grid (2.73 ha), two sides bounded by forest and the other two with a 7.5-m buffer of forest between a pastured thicket and cultivated field, respectively.

Weather permitting, I live-trapped each of these 420 stations weekly from 7 May to 4 October, with the exception of 7 July to 25 July.

Because the plots where *Peromyscus maniculatus* were captured were exceptionally uniform in structure, I discontinued trapping after obtaining a sufficient number of deer mouse captures (26) for analysis. In all study areas, traps were placed as close to station markers as possible. Using a random procedure, I selected a permanent direction for approach to each station. Over 5000 trap-nights were accumulated in all habitats (Table 1).

All animals captured were identified to species, weighed, aged, sexed, general and breeding condition noted, and trap location and capture status (newly marked or recapture) recorded. Animals were marked by toe clipping and metal ear tags.

DATA ANALYSIS AND HABITAT VARIABLES

Multiple discriminant function analysis, a technique that predicts species membership of individuals based on a set of continuous variables (Cooley and Lohnes, 1971), can be used to test for significant differences in microhabitat selection. Stepwise models, by maximizing the among- to within-groups sums of squares, sequentially extract those orthogonal variables most capable of separating species. There should be an a priori basis for selecting the environmental parameters entered into the analysis (Green, 1971); furthermore, these should have been reported in the literature as being important. Only habitat measures (or correlates of measures) previously found important in the ecological separation of small mammals at this latitude should be considered. These include the utilization of arboreal habitat, habitat structure and the amount of surface debris (M'Closkey and Fieldwick, 1975).

In order to quantify these important characteristics of the habitat, I measured (or derived from measures) 21 habitat variables per station (Table 2). To determine the horizontal foliage density readings (Q_1), a modified version of the coverboard technique of MacArthur and MacArthur (1961) and Rosenzweig and Winakur (1969) was used. At a constant distance of 1 m I recorded the proportion of a 5×10 cm "board" covered by vegetation on a quintile scale at 12.5-cm, 25-cm and at 25-cm intervals to 175 cm. I recorded these measures in the three major directions other than the one selected for approach to the trap station, and computed the mean value. Habitats were measured at the time when I judged them to have the greatest amount of vegetation present. The measures were combined into three height classes which roughly corresponded to a lower dense layer of short grasses and herbs, an intermediate layer of herbaceous vegetation and an upper layer of tall grasses and shrubs (M'Closkey and Fieldwick, 1975).

Mat depth (amount in cm of dead grasses, leaves and other debris on the soil surface) and vertical density (obtained by placing a profile board on the ground and

recording the proportion concealed by vegetation below 175 cm) were taken at 50- and 100-cm distances from each station along the same three axes as the horizontal densities, and mean values calculated for each. Tree species, tree numbers and basal area (as per Smith, 1974) were recorded within a radius of 7.5 m from each station. To gain more insight into the gross physiognomy of the plots, I measured the height of the first branch (for all trees) 50 cm in length or greater, and grouped the data for each station into five height classes (Table 2). Because *Peromyscus leucopus* uses horizontal branches as runways, I recorded the number of branches on the ground along the trap transect to 7.5 m on either side of the station, and also counted the number of logs and stumps within 7.5 m of each station as a measure of debris and possible nesting sites.

Square root and logarithmic transformations of the data were used where appropriate (Table 2).

RESULTS

A total of 477 animals of six native small mammal species were captured during the study period (Table 1). The number of species varied from two in the structurally and floristically simple agricultural plots, to a maximum of five in the savanna (Table 1).

An indication of macrohabitat preferences for these animals should be revealed by considering those species co-occurring in major habitat types (Table 1). The congeners, *Peromyscus leucopus* and *P. maniculatus*, the two potentially strongest habitat competitors, co-occurred only in one old-field (1.22 ha); however, *P. maniculatus* was restricted to the herbaceous areas and *P. leucopus* to overgrown fencerows, and the macrohabitat separation was maintained. *Peromyscus maniculatus* also never was captured in the same habitat as *Zapus* or *Blarina*, though in part this could be an artifact of minimum sampling in these habitats. *Tamias* is restricted to the open woods and savanna habitats, and is locally sympatric with all species except *P. maniculatus*.

TABLE 2.—Variables used for quantifying components of habitat structure

| Symbol | Description of variable |
|--------------|-----------------------------------------------------------------------|
| Q_1 | amount of vegetation from 0-0.25 m |
| Q_2 | amount of vegetation from 0.25-1 m |
| Q_3 | amount of vegetation from 1-1.75 m |
| ΣQ_i | amount of vegetation below 1.75 m |
| p_1 | proportion of vegetation in 0-0.25 m layer |
| p_2 | proportion of vegetation in 0.25-1 m layer |
| p_3 | proportion of vegetation in 1-1.75 m layer |
| FHD | foliage height diversity ($1/\Sigma p_i^2$) |
| MAT | mat depth (cm) |
| VERT | vertical vegetation density from 1.75 m |
| r_1 | proportion of trees with 1st branches from 0-1 m |
| r_2 | proportion of trees with 1st branches from 1-2 m |
| r_3 | proportion of trees with 1st branches from 2-3 m |
| r_4 | proportion of trees with 1st branches from 3-4 m |
| r_5 | proportion of trees with 1st branches from 4-5 m |
| BHD | branch height diversity ($1/\Sigma r_i^2$) |
| BASAL | \log_{10} tree basal area |
| TS | square root of the number of tree species |
| LOGS | square root of the number of logs and stumps within 7.5 m |
| BRANCH | square root of the number of branches 7.5 m both sides of the station |
| TN | square root of number of trees of all species |

TABLE 3.—Number of stations with single and mixed species captures

| Small mammal species | Small mammal species | | | | | |
|--------------------------------|----------------------------|-------------------------------|------------------------|--------------------------------|------------------------|---------------------------|
| | <i>Peromyscus leucopus</i> | <i>Peromyscus maniculatus</i> | <i>Tamias striatus</i> | <i>Microtus pennsylvanicus</i> | <i>Zapus hudsonius</i> | <i>Blarina brevicauda</i> |
| <i>Peromyscus leucopus</i> | 190 | | .. | .. | | .. |
| <i>P. maniculatus</i> | 0 | 22 | .. | .. | | .. |
| <i>Tamias striatus</i> | 9 | 0 | 7 | .. | | .. |
| <i>Microtus pennsylvanicus</i> | 0 | 3 | 0 | 7 | | .. |
| <i>Zapus hudsonius</i> | 2 | 0 | 0 | 1 | 11 | .. |
| <i>Blarina brevicauda</i> | 7 | 0 | 0 | 0 | 0 | 1 |

Patterns in microhabitat differences should become clear after examination of stations recording single and mixed species captures (Table 3). *Peromyscus leucopus* and *Microtus* never were captured at the same station, and the absence of *P. maniculatus*-mixed captures, except with *Microtus*, is the result of the macrohabitat differences.

Tamias and *Blarina* co-occurred only with *Peromyscus leucopus* while *Zapus* was occasionally taken at identical stations with either of *P. leucopus* or *Microtus*. At no station were three or more species captured. However, these data alone are not sufficient to determine microhabitat specialization. For example, seven out of eight *Blarina* were captured at stations also recording *P. leucopus* captures. Yet, the *P. leucopus* found at these stations may be in "suboptimal" habitats (at the tail of the *P. leucopus* habitat preference distribution) and the two species could recognize different microenvironments.

Use of stepwise discriminant function analysis based on species presence revealed significant overall microhabitat separation of all species pairs except *Zapus* and *Blarina* due to a combination of tree basal area, amount of vegetation between 0.25 and 1 m, number of trees, depth of dead grasses, leaves and other debris on the soil surface and the proportion of trees with first branches between 2 and 3 m ($F = 18.84$, $p < 0.001$) (Table 4).

Small sample sizes for some species may contribute to this separation. However, the three species with low sample sizes (*Blarina*, *Microtus* and *Zapus*) all were captured in a minimum of three different plots. This maximized the habitat preference distributions for these species, increased the variance in microhabitat selectivity, and made significant species separation more difficult. Thus, the microhabitat separation reported here is probably a valid reflection of natural differences, and not the result of biased sampling.

To determine structural habitat preferences of the six small mammal species, means and standard deviations for the five significant habitat variables are contrasted (Table 5). *Peromyscus leucopus* was abundant in areas with the most trees (TN), whereas *P. maniculatus* was found in treeless regions with little debris. *Tamias striatus* preferred habitats with few large trees, and a forest physiognomy represented by a high proportion of trees lacking branches below 2 m (r_1 and $r_2 = 0.01$ and 0.09 , respectively). *Zapus hudsonius* and *Blarina brevicauda* were associated with areas of high foliage density between 0.25 and 1 m, and *Blarina* also preferred a deep mat of debris. *Microtus* occurred in habitats with low but variable measures of debris and tree density.

TABLE 4.—Habitat separation based on F-ratios for species separation due to a combination of tree basal area, amount of vegetation between 0.25 m and 1 m, number of trees, depth of dead grasses, leaves, and other debris on the soil surface, and proportion of trees with first branches between 2 m and 3 m

| Small mammal species | Small mammal species | | | | |
|--------------------------------|----------------------------|-------------------------------|--------------------------------|------------------------|------------------------|
| | <i>Peromyscus leucopus</i> | <i>Peromyscus maniculatus</i> | <i>Microtus pennsylvanicus</i> | <i>Tamias striatus</i> | <i>Zapus hudsonius</i> |
| <i>Peromyscus maniculatus</i> | 92.53** | | | | .. |
| <i>Microtus pennsylvanicus</i> | 10.60** | 11.36** | | | .. |
| <i>Tamias striatus</i> | 14.80** | 50.03** | 14.54** | | .. |
| <i>Zapus hudsonius</i> | 3.61* | 30.14** | 3.14* | 12.22** | .. |
| <i>Blarina brevicauda</i> | 3.19* | 31.22** | 6.88** | 6.69** | 1.70 ns |

* $p < 0.01$, ** $p < 0.001$

The habitats that I have censused contain from two to five native small mammal species (Table 1) and it is necessary to account for these differences. Variation in habitat availability (variable total niche space) is one factor that may explain the observed variation in species density among habitats. Important habitat measures should be those significant variables from the discriminant analysis. Thus habitat availability for a particular study plot is equal to the mean value of each of the five significant variables over all stations recording captures in that habitat. Linear regression of these measures of habitat availability against the species density values of Table 1 gave one significant relationship, where species density can be predicted from mean mat depth ($r = 0.89$, $p < 0.02$).

Since all species pairs but *Blarina-Zapus* select different microhabitats (Table 4), I postulated that increased habitat heterogeneity might also be a good predictor of increased species number. One very good measure of habitat heterogeneity is the degree of variation among stations of the significant variables in the discriminant analysis. No significant relationships were found by linear regression.

MacArthur (1972), among others, has shown the importance of the vertical habitat component in predicting bird species diversity. Because two of the small mammal species in this study are at least partially arboreal (*Peromyscus leucopus*, *Tamias*), the complexity of the vertical habitat could have the same effect on increased species density as that postulated for the coefficients of variation of the significant habitat variables. The overall complexity of the vertical component of habitat structure per habitat type is the mean value of FHD over all stations in that habitat where animals were captured. The resulting linear regression of mean FHD vs. small mammal species density was significant ($r = 0.83$, $p < 0.05$).

DISCUSSION

The habitat requirements of the small mammal community are consistent with those previously reported for this region (M'Closkey, 1975b; M'Closkey and Fieldwick, 1975; M'Closkey and Lajoie, 1975; and others referred to by M'Closkey and Fieldwick, 1975). There was no evidence of microsympatry between *Microtus* and *Peromyscus leucopus* as demonstrated by M'Closkey (1975b) and M'Closkey and Fieldwick (1975). This may be due to the low population density of *Microtus* during 1975.

M'Closkey (1975b) and M'Closkey and Fieldwick (1975) have shown that *Microtus* and *Peromyscus leucopus*, when captured alone, select significantly different microhabitats, as well as being ecologically separated by macrohabitat differences. Furthermore, the microhabitat values at mixed species stations were significantly

TABLE 5.—Mean values for the five significant discriminating structural habitat variables (standard deviations in parentheses)

| Small mammal species | BASAL | Structural habitat variable | | | r_3 |
|--------------------------------|----------------|-----------------------------|----------------|----------------|----------------|
| | | Q_2 | TN | MAT | |
| <i>Peromyscus leucopus</i> | 2.86 (1.41) | 1.34 (1.08) | 3.61 (2.38) | 2.70 (1.75) | 0.19 (0.24) |
| <i>P. maniculatus</i> | 0.00 (0.00) | 0.09 (0.25) | 0.71 (0.00) | 0.32 (0.43) | 0.00 (0.00) |
| <i>Tamias striatus</i> | 3.54 (0.24) | 1.37 (0.66) | 1.82 (0.53) | 3.74 (1.55) | 0.66 (0.31) |
| <i>Microtus pennsylvanicus</i> | 0.63 (1.02) | 1.76 (1.38) | 0.93 (0.32) | 2.17 (1.75) | 0.00 (0.00) |
| <i>Zapus hudsonius</i> | 1.28 (1.73) | 2.12 (1.17) | 1.96 (2.21) | 3.40 (1.51) | 0.04 (0.08) |
| <i>Blarina brevicauda</i> | 1.74 (1.87) | 2.16 (1.47) | 2.11 (2.22) | 4.71 (2.32) | 0.24 (0.35) |

different from those where either species was captured singly, and thus are a reflection of the macrohabitat separation. McCloskey suggested that because only transient *Microtus* were captured at mixed census stations, these locations represent marginal vole habitat. This conclusion is substantiated by my results in identical habitats, but under much lower vole density, of only macrohabitat separation between *P. leucopus* and *Microtus*. This is consistent with the hypothesis that under high population density some *Microtus* individuals are forced into suboptimal habitats (Christian, 1970; Krebs and Myers, 1974). Dispersers are often thought to be young animals, and in this regard it would be interesting to know the relative ages of the *Microtus* at mixed species stations, compared to the ages of those at stations where only voles were captured.

The significant habitat separation of all species except *Blarina* and *Zapus* is suggestive that habitat competition may be occurring among this set of small mammal species. One way of ascertaining if these species are truly competitors, and that the observed differences are not the result of independent niche evolution, would be through species removal experiments and monitoring equilibrium population densities and habitat resource utilization of the remaining species in the community. If the removed species are competitors of those species remaining, then population expansion and perhaps increased habitat utilization should occur in their absence. Note, however, that absence of an expansion of equilibrium densities of these species (even under ideal and constant conditions) does not eliminate the possibility that competition was important in the evolution of the reported differences. Schroder and Rosenzweig (1975) have recently shown that removal experiments of this type can be effectively executed on small mammal populations. Future studies substantiating the extent of competition for limited resources in this assemblage of mammals should also incorporate concurrent data on food resource utilization.

Intuitively, the competition hypothesis can be given second billing to the alternate hypothesis of long-term independent evolution resulting in microhabitat segregation. This conclusion is based on conspicuous differences among the species rather than on direct evidence of independent evolution. Is it not as equally improbable that microhabitat segregation is related to competition as it is that major differences such as herbivory in *Microtus* and insectivory in *Blarina* are the net results of previous competitive interactions among prehistoric voles and shrews? Other important dissimilarities, such as seasonal hibernation in *Zapus* and *Tamias* as well as diurnal activity in *Tamias*, tend to discount the importance of competition in the evolution of the habitat differences. It is more likely that the observed microhabitat preferences are related to foraging and dietary differences of the small mammals.

Neither *Zapus* nor *Blarina* coexisted with deer mice in major habitat types, and this necessarily created large F-ratios for microhabitat separation. *Zapus* is ubiquitous, but is primarily an old-field, grassland species, and prefers moist areas (Getz, 1961). The agricultural plots and old-fields recording deer mouse captures all were drained artificially, and may not meet the environmental requirements of jumping mice. By comparison, Quimby (1951) has documented some habitat overlap of *Zapus hudsonius* with *Peromyscus maniculatus bairdii* in Minnesota. The high degree of structural habitat separation of these species reported here may be an exaggeration of natural differences between them, due to agricultural drainage of otherwise acceptable *Zapus* habitats.

Of the five rodent species, *Peromyscus maniculatus* is the most insectivorous. Bernyk (1975), working with *P. maniculatus bairdii* in Point Pelee National Park, has reported as much as 77% of the diet to be insect material. On the basis of high potential food overlap, habitat segregation between deer mice and shrews tends to substantiate a competition hypothesis. However, Grant (1976) in a long-term study

of small mammal populations in southern Quebec, has found these two species to be locally sympatric. Several possible explanations for the differences between my results and Grant's come to mind. First, macrohabitat separation between *Blarina* and *P. maniculatus* may be caused by historical agricultural practices as appears to be the case for deer mice and jumping mice; or second, I may have studied the populations during a period of temporal differences in microhabitat preference. Temporal separation should be related to population densities of the two species. Another explanation is that Grant's study areas represent an interface of acceptable *P. maniculatus* and *Blarina* microhabitats. Alternatively, regional *P. maniculatus* and/or *Blarina* populations may have evolved habitat preferences suitable to regional geographic areas, but different from the habitats selected by other regional populations. Dependent upon local or regional conditions the two species could independently evolve either similar or divergent habitat affinities.

Blarina and *Zapus*, the only species occurring in statistically equivalent microhabitats, belong to different orders, and are of very divergent morphologies. *Blarina* is semifossorial, while *Zapus* frequently uses a form of bipedal locomotion. In addition, *Zapus* is primarily a granivore (Getz, 1961; Quimby, 1951), and should compete little for food with *Blarina*.

Of the five measures of resource availability, only mat depth is a good predictor of small mammal species density in southwestern Ontario. Both *Microtus* and *Blarina* make use of extensive runway systems in the mat, and it is interesting to note that these species co-occurred only in the savanna, which recorded the highest values for both species density and mat depth. Miller and Getz (1977) have postulated that moist environments are important in habitat selection by small mammals. Water content of the litter layer should be some increasing function of mat depth and may serve to reduce the evaporative water loss of small mammal occupants. Mat depth is also probably a correlate of productivity available to the small mammal community. In the agricultural plots (lowest species density and mat depth), productivity is high, but is harvested before it is readily available to small mammals, while the forest productivity is tied up in increased biomass of the plant community. In the savanna, most of the plant biomass (except for infrequent trees and shrubs) is added to the mat annually. This available productivity, the suitability of the mat for runway construction and its importance in reducing evaporative water loss are likely the important features of mat depth recognized by small mammals.

Most measures of habitat heterogeneity (coefficients of variation of the significant variables from the discriminant function analysis) are not correlated with species density in these communities, but another measure of habitat variation, vertical habitat complexity (mean foliage height diversity), is significantly correlated with species number. This is noteworthy because the most diverse community has three species (*Microtus*, *Zapus* and *Blarina*) for which arboreal activity has not been reported. However, *Tamias* is somewhat arboreal (Burt, 1948, 1972), and *Peromyscus leucopus* makes extensive use of above-ground vegetation (M'Closkey, 1975a, 1976) and often nests in trees (Nicholson, 1941). A similar correlation has been reported by MacArthur (1972) and MacArthur and MacArthur (1961) between foliage height diversity and bird species diversity. The responses of small mammals and birds to foliage height diversity are probably not the same. Birds, theoretically, can utilize discrete layers independent of one another, whereas arboreal small mammals must show differential utilization of layers with a great deal of overlap among species (all are captured on the ground). It is best, when dealing with mammalian communities, to consider vertical habitat complexity only as another measure of habitat heterogeneity.

I cannot overemphasize the extreme caution required in interpreting the

biological meaning of multivariate statistical procedures. Statistical significance of microhabitat differences does not necessarily imply that the animals actively search out different microhabitats. Rather, these tests can only be used to demonstrate statistically significant differences in microhabitat separation, independent of the causal agents of that separation. Note that this does not detract from the scientific merit of the work in determining the repeated patterns of small mammal species distribution in microhabitat space. This study shows that microhabitat structure can be used to predict species distributions in a local small mammal fauna. Different small mammal species in southwestern Ontario do live in different microenvironments.

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