Microhabitat Separation and Coexistence of Two Temperate-zone Rodents

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Microhabitat separation of White-footed Mice (*Peromyscus leucopus*) and Meadow Voles (*Microtus pennsylvanicus*) was analyzed within two macrohabitats in Point Pelee National Park. Foliage height diversity, an important predictor of habitat separation by Mice and Voles in macrohabitat studies, was unimportant when the separation was analyzed within habitats. Significant microhabitat separation between White-footed Mice and Meadow Voles reflected macrohabitat preferences, but the separation was dynamic, and no single variable consistently accounted for microhabitat differences. The coexistence of Mice and Voles appears to depend upon microhabitat differences which are maintained despite frequent shifts in microhabitat use by each species.

Key Words: discriminant analysis, habitat selection, microhabitat, *Microtus pennsylvanicus*, Ontario, *Peromyscus leucopus*.

White-footed Mice (*Peromyscus leucopus*) and Meadow Voles (*Microtus pennsylvanicus*) usually occupy different habitat types, but they are occasionally sympatric in ephemeral habitats (M'Closkey and Fieldwick 1975; Morris 1980, 1983). This short-term coexistence suggests that within preferred habitats, site selection by individuals of each species is determined by within-habitat variation. Consequently, the distribution of these species should be predictable by microhabitat, with the result that macrohabitat allopatry is itself an outcome of microhabitat preference.

M'Closkey (1975) reported such an apparent pattern in Point Pelee National Park. Live-trapping censuses of several habitats revealed three distributional patterns of Mice and Voles: White-footed Mice only; Meadow Voles only; and mixed habitats with resident White-footed Mice and transient Meadow Voles. M'Closkey used analysis of variance to demonstrate that pairs of rodent habitats were structurally different in terms of foliage height diversity (FHD), a measure of variation in the horizontal layering of vegetation. White-footed Mice lived in structurally more diverse habitats than the Meadow Voles. This microhabitat separation reflected the different physiognomies of the Mouse and Vole habitats, but revealed little about the importance of FHD as a predictor of Meadow Vole and White-footed Mouse distribution within mutually acceptable macrohabitats.

If local allopatry between White-footed Mice and Meadow Voles is a reflection of microhabitat selection by individuals, and if FHD determines the pattern of habitat separation by mice and voles, then within mixed-species habitats, species separation on the basis of FHD should be maintained. M'Closkey and Fieldwick (1975), in a wet prairie community, analyzed habitat differences between mice and voles by discriminant function analysis, and found significant species separation accounted for by a combination of FHD, tree basal area, and the depth of surface litter. The prairie is far from homogeneous, however, and ranges from "treeless areas of grass to wooded, fern covered localities" (M'Closkey and Fieldwick 1975). The importance of FHD in separating species may be as much the result of physiognomic differences between mouse and vole macrohabitats, as it is the result of an important structural cue to microhabitat selection. The relative importance of these two scales of habitat selection remains unresolved. If microhabitat separation accounts for macrohabitat preference, then similar variables should be responsible for species separation at both scales of habitat analysis.

This report analyzes microhabitat separation between White-footed Mice and Meadow Voles within old field and grassland mixed-species habitats. It asks: Are the patterns of White-footed Mouse and Meadow Vole macrohabitat use consistent with microhabitat separation within macrohabitats? Do the same sets of structural variables consistently account for species separation?

Field Sites and Methods

Small mammals were live-trapped and vegetation structure quantified in grassland, old field, sumac regrowth and deciduous forest habitats in Point Pelee National Park, Ontario (42° 00'N, 82° 31'W). White-footed Mice resided in both the sumac and forest; Meadow Voles were absent in the sumac and transient in the forest. Both species co-occurred in a 10-yr-old field overgrown with brambles (*Rubus* sp.), goldenrod (*Solidago* spp.) and Tufted Vetch (*Vicia cracca*) with invading saplings of Ash-leaved Maple (*Acer negundo*) and Red Osier Dogwood (*Cornus stolonifera*); and in a grassland of Wheat Grass (*Agropyron trachycaulum*) with a few young White Pine (*Pinus strobus*) saplings and dense clumps of Black Locust (*Robina pseudoacacia*) suckering from removed parent trees.

In both habitats, single Longworth live-traps were placed at the intersections of a 9 × 15 grid (15 m trap spacings) in the evening, and checked and removed at first light the next day. From 3 May to 10 November 1978, and from 16 May to 29 October 1979, every third line was live-trapped at approximately 10-day intervals, with all 270 stations being trapped six times in each of 1978 and 1979 (810 trap nights in each habitat per year). Each individual captured was identified to species and all rodents were individually marked with metal ear tags, aged, sexed, reproductive status recorded, measured, trap station registered and capture status noted (newly marked or recapture). Animals were released at the point of capture immediately after processing. All soiled traps were washed in detergent and thoroughly rinsed before being reset.

Microhabitat was quantified at all stations. Structural characteristics (two measures each of horizontal profiles, and four of vertical density and surface litter: Morris 1979) were recorded in both 1978 and 1979, and measures of woody perennials (distance in m to the nearest tree, sapling and shrub) as well as shrub numbers within three m, were recorded in 1978. Appropriate data transformations were used where necessary, and all variables were screened for homogeneity (unimodal and symmetrical distribution of scores) and redundancies prior to analysis (Table 1).

Stepwise multiple discriminant function analysis (Wilks method, Klecka 1975) evaluated microhabitat separation within habitats and years. I used a conservative approach where discriminating variables were included in the analysis if they significantly contributed to species separation at $p < 0.05$; they were excluded at $p > 0.025$.

Input for the discriminant analyses were the capture frequencies of each species recorded at each trap station. Species presence could also be used (eg. Morris 1979), but capture frequencies should give a more complete description of the probability density functions of microhabitat use. Before analyzing for differences in microhabitat use, I looked for species differences in residency. If the proportion of transients within a habitat differed between species, the analysis might not detect significant differences in microhabitat as much as it would reflect sampling bias of transient individuals moving through the habitat.

Results

A total of 148 White-footed Mouse and 487 Meadow Vole captures were recorded in the two years of the study (Table 2). Recapture frequencies between species and within habitats and years were similar (Table 2), indicating that the proportion of transient to resident animals was the same for both species. Neither group contributed disproportionately to microhabitat separation by discriminant analysis.

White-footed Mice and Meadow Voles used significantly different microhabitats within each habitat in both 1978 and 1979 (Table 3). In no instance was FHD a significant contributing variable to species separation.

As M'Closkey (1975) predicted, White-footed Mouse microhabitats were structurally more diverse, as measured by FHD, than those of the Meadow Vole (Table 4). The importance of this relationship is overshadowed by voles in the old field occupying areas of greater foliage height diversity than did White-footed

TABLE 1. Quantitative variables used in the analysis of *Peromyscus-Microtus* microhabitat separation in the grassland and old field habitats at Point Pelee National Park.

Variable	Description
Q1	Amount of vegetation from 0–0.25 m
Q2	Amount of vegetation from 0.25–1 m
SUMQ	Total vegetation below 1.75 m
FHD	Foliage height diversity ($1/\Sigma p_i^2$)
AP1	Arcsin proportion vegetation in 0–0.25 m layer
AP2	Arcsin proportion vegetation in 0.25–1 m layer
VERT	Vertical vegetation density from 1.75 m
DVERT	Vertical density diversity among replicate measures
LMAT	Log_{10} mat depth
CMAT	Coefficient of variation of LMAT among replicates
STDEN	Square root of distance to nearest tree > 10 cm dbh
SSDEN	Square root of distance to nearest sapling
SBDEN	Square root of distance to nearest shrub
BUSHN	Square root of shrub numbers within 3 m

TABLE 2. Total *Peromyscus* and *Microtus* captures in equal-sized plots in grassland and old field habitats at Point Pelee National Park. Recapture frequencies are in parentheses.

	Habitat			
	Grassland		Old Field	
Species	1978	1979	1978	1979
Peromyscus	18 (0.44)	18 (0.39)	18 (0.39)	94 (0.59)
Microtus	142 (0.32)	233 (0.37)	39 (0.33)	73 (0.59)

Mice in the grassland. Despite this complexity, there are some patterns in microhabitat preference. White-footed Mice were consistently captured in areas of greater tree and shrub density than were Meadow Voles, even though these differences were not always statistically significant (Table 4).

Discussion

Microhabitat separation within habitats reflected differences in macrohabitat use by mice and voles. White-footed Mouse microhabitats had more total vegetation and greater densities of woody perennials than Meadow Vole microhabitats. Meadow Voles, on the other hand, were captured in areas with more plant litter than were White-footed Mice. The local distribution of White-footed Mice and Meadow Voles seems to depend upon microhabitat selection by individuals. But the pattern of microhabitat selection is not easily defined. No single structural variable was a consistent descriptor of species separation, and compound structural variables may not provide better descriptors of microhabitat differences (Morris, 1980). Discriminating variables may also change in the direction of separation between habitats. In 1979, White-footed Mice in the grassland were caught in microhabitats characterized by a higher proportion of vegetation in the 0.25 – 1 m layer (AP2) than were Meadow Voles. In 1978, however, Meadow Voles in the old field were captured in areas with greater AP2 than were White-footed Mice (Table 4). This likely means that microhabitat selection by individuals is variable, and that patterns of microhabitat use are influenced by the degree of environmental variability encountered in a given macrohabitat.

The tree and shrub density differences demonstrated that within the two mutually acceptable habitats, White-footed Mice were associated with brush and briars, whereas the Meadow Voles were more often found in field openings. The preference of Mice for shrubby and wooded sites, and the Meadow Vole's complementary association with open areas, probably accounts for the usual allopatric distributions of these species.

Previous studies of ecological separation between mice and voles predicted that the two rodent species should occur in microhabitats differing in foliage height diversity. Stepwise multiple discriminant function analysis between these species in the old field and grassland habitats confirmed microhabitat separation, but unlike M'Closkey's results, foliage height diversity was not a discriminating variable. M'Closkey (1975) evaluated structural habitat use across successional habitats. As White-footed Mice are most frequent in shrub and forest habitats, and Meadow Voles are most abundant in open canopy old fields and grasslands, it was predictable that measures of foliage profiles would be different for the two species at this scale of analysis (see also Morris 1984a). The scale of inquiry into habitat separation profoundly affects the outcomes of analyses of habitat separation (Morris, 1984b). Variables responsible for species separation within habitats may not be those same variables which are most capable of separating macrohabitat types.

Variability in microhabitat separation in this study is emphasized in two different ways. First, only one of the discriminating variables was repeated between habitats. Second, even within habitats, discriminating

TABLE 3. *Peromyscus-Microtus* microhabitat separation by stepwise multiple discriminant function analysis in two habitat types in Point Pelee National Park.

Habitat	Year	F-ratio	Discriminating Variables
Grassland	1978	28.03**	LMAT, SUMQ
Grassland	1979	10.42**	AP2, SUMQ, SBDEN
Old Field	1978	6.44*	Q1, AP2
Old Field	1979	24.64**	Q1, BUSHN, STDEN

* $0.01 > p > 0.001$; ** $p < 0.001$

TABLE 4. Mean values of the microhabitat variables used in *Peromyscus-Microtus* separation in grassland and old field habitats at Point Pelee National Park.

	Peromyscus				*Microtus*			
	Grassland		Old Field		Grassland		Old Field	
Variable	78	79	78	79	78	79	78	79
Q1	4.39	4.41	4.01*	3.81*	4.39	4.57	4.36*	4.29*
Q2	1.86	2.54	2.99	2.86	1.62	1.84	3.40	3.09
SUMQ	6.31*	7.01*	8.01	7.79	6.02*	6.69*	8.25	8.03
FHD	1.70	1.84	2.26	2.29	1.63	1.73	2.15	2.15
AP1	57.01	53.01	46.77	46.13	59.31	57.99	47.20	48.22
AP2	32.01	36.57*	37.53*	36.85	30.58	30.38*	39.65*	37.73
VERT**			3.79	4.03			4.42	4.29
DVERT	3.53	3.85	3.83	3.80	3.59	3.65	3.88	3.83
LMAT	0.34*	0.43	0.20	0.36	0.59*	0.42	0.29	0.42
CMAT	53.60	67.44	45.05	52.51	41.29	52.38	60.28	46.89
STDEN	4.94	5.56	4.90	4.98*	5.44	5.63	5.78	5.69*
SSDEN	2.12	2.31	1.21	1.07	2.13	2.18	1.09	0.96
SBDEN	1.08	0.84*	1.15	1.01	1.82	1.80*	1.31	1.23
BUSHN**			2.44	2.65*			2.14	2.02*

*A significant variable in species' microhabitat separation.
**VERT and BUSHN did not meet screening requirements in the grassland.

variable sets were not constant between years, as both vegetation structure and rodent microdistribution changed (Morris, 1980). These results show that microhabitat differences between Mice and Voles occur even within homogeneous habitats, that the separation is not a statistical quirk of heterogeneous sampling, and that the separation is dynamic in space and time. The coexistence of White-footed Mice and Meadow Voles does not result in interspecific competition (Morris, 1983), but appears instead to reflect preferences in microhabitat selection which are different, but malleable and easily shaped to varying environments.

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