# Patterns and scale of habitat use in two temperate-zone, small mammal faunas

Douglas W. Morris

*Department of Biology, Memorial University of Newfoundland, St. John's, Nfld., Canada A1B 3X9*

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Small mammals were livetrapped and habitat quantified in replicates of six macrohabitats in Alberta and in temporal replicates of four macrohabitats in Ontario, Canada. Similar patterns emerged in both locations. The relative abundances of small mammals depended upon macrohabitat; within macrohabitats, species differed significantly in microhabitat use. The patterns were dynamic and probably the result of habitat preference instead of species interactions. Macrohabitat differences may in part be outcomes of microhabitat selection, but are unlikely to be completely understood without superimposing colonization and extinction probabilities on habitat selection models. Field biologists must recognize both scales of habitat to interpret patterns of species distribution.

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Les petits mammifères ont été capturés vivants en six macrohabitats semblables d'Alberta et leur nombre a été évalué; les petits mammifères ont également été capturés aux mêmes fins, mais dans des conditions temporelles identiques, en quatre macrohabitats d'Ontario, Canada. Aux deux endroits, les populations ont les mêmes tendances. L'abondance relative des petits mammifères dépend du macrohabitat et, au sein d'un macrohabitat, les espèces utilisent les microhabitats de façons significativement différentes. Ces patterns sont dynamiques et résultent probablement des préférences spécifiques d'habitat plutôt que d'interactions spécifiques. Les différences entre les macrohabitats résultent sans doute en partie de la sélection des microhabitats, mais il semble impossible de comprendre entièrement ces mécanismes sans avoir au préalable tenté de confronter les probabilités de colonisation et d'extinction aux modèles de sélection d'habitat. Les biologistes doivent tenir compte des deux échelles d'habitat pour pouvoir interpréter la répartition de l'espèce.

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## Introduction

Habitat separation commonly facilitates the cooccurrence of similar species (Schoener 1974; Rosenzweig 1981). For habitat specialists, the diversity and abundance of habitat types may determine the diversity and abundance of those specialist species. Habitat specialists may arise through independent evolution in heterogeneous environments, but may also have been restricted in habitat use by competitors. Competition within species should tend to cause an expansion of the variety of habitats used (Svardson 1949; Fretwell and Lucas 1970; Grant 1975). This expansion may be opposed by the inhibitory effects of interspecific competitors (Svardson 1949; Grant 1975), and theoretically, the contraction should lead to predictable patterns of habitat use in multispecies systems (MacArthur and Levins 1964; Rosenzweig 1979; Pimm and Rosenzweig 1981).

These theories rely on the assumption that different habitats are recognized as patches by the animals which live in or move among them. The size of the patches profoundly influences strategies of habitat use. When patch size is large relative to the movements of individuals (a so-called coarse-grained environment (MacArthur and Levins 1964)), individual animals use only that single patch. But when patch size is small relative to the movements of individuals (a fine-grained environment), individuals can either use all patches, and functionally increase patch size, or continue to use some preferentially over others, but be forced to pass through unfavourable patches.

These possibilities create great problems for field biologists. If we examine a variety of large patch types relative to the movements of constituent species (macrohabitats for those species), and find that each has a particular species associated with it, we may assume that these species prefer certain habitats over others. If we find species using several macrohabitats, we may assume they are opportunistic in habitat use. But within

these large patches, individuals may preferentially use some areas (microhabitats) more than others, or they may be using all areas equally. Further problems of interpretation arise when groups of similar species occur in one or more large habitat patches. Are all of the species selective or opportunistic in habitat use, or some mixture of the two? Clearly any successful analysis of habitat preference and species coexistence must identify the scale of habitat use by cooccurring species, and be able to evaluate the importance of the different scales to species distribution (Morris 1984).

Most studies of cooccurring small mammals have documented some form of microhabitat preference among species (e.g., North American temperate-zone species; M'Closkey 1975; M'Closkey and Fieldwick 1975; Dueser and Shugart 1978; Morris 1979; Vickery 1981). But most of these studies too have mixed macrohabitat and microhabitat effects. Frequently, species are captured in a variety of macrohabitats, microhabitat quantified in some way, and then species are analyzed for microhabitat separation by lumping the data from all macrohabitats censused. This is a valid approach only if two conditions are met. First, all species being compared should show no selectivity across the spectrum of macrohabitats sampled. Second, the distribution of the microhabitat variables should be continuous across macrohabitats. Few if any studies of habitat selection by small mammals have carefully disentangled these effects. Habitat analyses of other groups of organisms face similar difficulties (recent examples include Holmes et al. 1979 (passerines); Lister 1981 (lizards); Nudds 1983 (waterfowl).

To make sense out of habitat distributions it seems necessary to evaluate consistently the relative influences of macro- and micro-habitat preference. When these results are compared with studies on other organisms, or with geographical comparisons of similar species, general rules of the scale of habitat

preference should emerge. This paper documents such a geographical comparison of two temperate-zone, small mammal faunas.

## Study areas

Small mammals were livetrapped in each of two 0.81-ha replicates of six habitats in the Kananaskis Valley of the Rocky Mountains, southern Alberta, and in 2.5-ha plots of four habitats in Point Pelee National Park, southern Ontario.

In Alberta, the mature forest plots were dominated by large white spruce (*Picea glauca*) with smaller numbers of Douglas and alpine fir (*Pseudotsuga menziesii, Abies lasiocarpa*). Green alder (*Alnus crispa*) was the most prevalent bush. Buffalo berries (*Shepherdia canadensis*) and gooseberries (*Ribes oxyacanthoides*) were the only other common shrubs. Violets (*Viola adunca*), twin flowers (*Linnaea borealis*), and bunchberry (*Cornus canadensis*) grew on a thick moist mat of mosses and forest litter.

The young spruce replicates were mainly composed of dense stands of white spruce with only a few lodgepole pine (*Pinus contorta*) and sparse willows (*Salix* sp.). Juniper (*Juniperus communis* and *J. horizontalis*), buffalo berry, dwarf birch (*Betula glandulosa*), and shrubby cinquefoil (*Potentilla fruticosa*) dominated the understory vegetation. A scattering of twin flowers, wild strawberry (*Fragaria glauca*), white camas (*Zygadenus elegans*), and an occasional false Solomon's seal (*Smilacena racemosa*) grew in well-developed mats of mosses and debris. Bearberry (*Arctostaphylos uva-ursi*) was common on exposed dry slopes.

Transition forests were more diverse with large numbers of mature aspen (*Populus tremuloides*), poplar (*P. balsamifera*), lodgepole pine and white spruce, and a few young alpine fir. Buffalo berries, common juniper, and wild roses (*Rosa* sp.) made up most of the woody understory. Bearberry, meadow rue (*Thalictrum venulosum*), violets (*Viola adunca* and *V. rugulosa*), wild lily of the valley (*Maianthemum canadense*), wild strawberry, and twin flowers grew in generally shallow litter.

The lodgepole forest was the least diverse habitat type. Almost all of the trees were lodgepole pine. Large and abundant alder bushes presented a formidable understory. Bunchberries and twin flowers covered a medium mat of mosses and litter.

Aspen forest, too, was very homogeneous consisting primarily of old, but dense, aspen clones mixed with poplar and an infrequent small white spruce. Saskatoons (*Amelanchier alnifolia*), wild roses, and buffalo berry represented common interspersed shrubs. Fireweed (*Epilobium angustifolium*), wild strawberry, meadow rue, and cow parsnip (*Heracleum lanatum*) grew well in the dense forest with bearberry being common in exposed areas. The litter layer was shallow.

Recent clear-cuttings were devoid of trees. Stumps and slash were left behind by loggers. Green alder, willow, wild raspberry (*Rubus strigosus*), buffalo berry, shrubby cinquefoil, and gooseberry provided an almost continuous luxuriant growth of shrubs. Numerous small lodgepole pine and aspen seedlings were becoming established. Fireweed, arnica (*Arnica* sp.), and bunchberry were common herbs. The mat was undeveloped.

In Ontario, the mature forest had a diverse mixture of large trees including hackberry (*Celtis occidentalis*), red cedar (*Juniperus virginiana*), silver maple (*Acer saccharinum*), and cottonwood (*Populus deltoides*) with an understory of deciduous saplings, chokecherry (*Prunus virginiana*), riverbank grape (*Vitis riparia*), and Virginia creeper (*Parthenocissus quinquefolia*). Adjacent to the forest was an old field densely covered with goldenrod (*Solidago* spp.), wild strawberries (*Fragaria virginiana*), brambles (*Rubus* sp.) and tufted vetch (*Vicia cracca*). This field was being colonized by red osier dogwood (*Cornus stolonifera*) and saplings of ash-leaved maple (*Acer negundo*) and cottonwood. Abutting the old field was a sumac stand which also developed from an abandoned field, and consisted of staghorn sumac (*Rhus typhina*) and red osier dogwood among which several young red cedar were becoming established. Riverbank grape was common throughout, and brambles were the most abundant

shrub. The fourth habitat was a wheatgrass (*Agropyron trachycaulum*) grassland with interspersed patches of poison ivy (*Rhus radicans*), riverbank grape, common and rough horsetail (*Equisetum arvense* and *E. hyemale*), and a few young white pine (*Pinus strobus*). Thick clumps of another introduction, black locust (*Robina pseudoacacia*), were suckering from removed parent trees, and a pair of overgrown fencerows protruded partway into the grassland plot.

## Methods and analysis

Single Longworth live-traps baited with oatmeal and peanut butter with apple or potato slices for moisture and mattress stuffing for insulation, were placed within 1 m of permanently marked intersections of 15 × 15 m grids. In Alberta, traps were set on alternate traplines during the evening, checked at first light and midevening the next day, and then collected at first light on the 2nd day. Each station was monitored in this manner three times from 16 May to 31 August 1977. In Ontario, traps were set in the evening and collected at first light. Each station, with the exception of a few subject to spring flooding in the forest, was monitored at six more or less monthly intervals from 3 May to 10 November 1978, and at six similar intervals from 16 May to 29 October 1979. Each interval consisted of three trap rotations where every third line was trapped on any given evening. The subsequent rotation trapped the adjacent line, so that each station was censused once each interval. In both locations, soiled traps were washed with detergent and rinsed with clean water before being moved to another station.

Habitat structure was quantified at every station. I selected a complex of variables which together would reflect microhabitat structure (Tables 1 and 2). Variables included estimates of forest density, biomass, and composition (TN, TD, TSD, SIZD, STDEN, BASAL), horizontal profiles, profile diversity, and vertical density as per Morris (1979) (Q1, Q2, Q3, SUMQ, DIV, AP1, AP2, AP3, VERT, DVERT), the mean of four randomly located estimates of accumulated litter (LMAT), and variability of litter depth at a given station (CMAT). Shrub density and dispersion in Alberta were estimated by counts and shrub volume (BN, BD, BVL, BVD, SAP) and in Ontario by counts and distance measures (SSDEN, SBDEN, BUSHN). In Alberta, surface litter was estimated by four randomly located $0.1\text{-}m^2$ cover plots within 1 m (AGRASS, ALITTER, AWOOD), and potential nest sites were recorded by counts of fallen logs, stumps, logs, and rocks (DEBRIS). All diversity variables were calculated using the inverse of Simpson's index ($1/\Sigma p_i^2$). SIZD was calculated by first classifying trees to the following seven basal area (square centimetres) categories: $0 < \text{SIZ1} < 50, 50 < \text{SIZ2} < 100, 100 < \text{SIZ3} < 200, 200 < \text{SIZ4} < 400, 400 < \text{SIZ5} < 800, 800 < \text{SIZ6} < 1600, 1600 < \text{SIZ7}$. BVD was calculated similarly by first classifying bushes to seven volume (cubic metres) categories: $0 < \text{BV1} < 0.25, 0.25 < \text{BV2} < 0.50, 0.50 < \text{BV3} < 1.00, 1.00 < \text{BV4} < 2.00, 2.00 < \text{BV5} < 4.00, 4.00 < \text{BV6} < 8.00, 8.00 < \text{BV7}$. Appropriate data transformations were undertaken where necessary (Tables 1 and 2), and only variables whose frequency distributions were unimodal and more or less symmetrical were used in subsequent analyses.

Species dependence on macrohabitat was evaluated by stepwise $\chi^2$ tests of quasi-independence in two-way frequency tables (BMDP P2F procedure; Brown 1979). This test sequentially identifies and excludes cells in the species × habitat data array that contribute the most to the dependence structure of species abundance on habitat. The analysis stops when the calculated $\chi^2$ of the remaining cells is no longer statistically significant ($p < 0.05$, in this case). The pattern of cell exclusion indicates which species and habitat comparisons are responsible for the lack of independence in the original cross-classification table. In this way, I can show not only whether species abundances depend upon macrohabitat, but can also rigorously identify which species–habitat combinations have unusual abundances.

Microhabitat separation among species within macrohabitats was determined by stepwise multiple discriminant functions analysis (Wilks method; Klecka 1975). Variables responsible for species separation were sequentially extracted relative to their ability to max-

TABLE 1. Variables used for quantifying microhabitat structure in 12 plots of six macrohabitats in the Kananaskis Valley

| Variable | Description | Plot[a] |
|---|---|---|
| Q1 | Amount of vegetation from 0 to 0.25 m | All but C1 |
| Q3 | Amount of vegetation from 1 to 1.75 m | F2 |
| SUMQ | Total vegetation below 1.75 m | All |
| AP1 | Arc sine of the proportion of vegetation in the $0-0.25$ m layer | All |
| AP3 | Arc sine of the proportion of vegetation in the $1-1.75$ m layer | F2 |
| VERT | Vertical vegetation density from 1.75 m | All but C1 |
| DVERT | Vertical density diversity | All |
| LMAT | $Log_{10}$ mat depth | All |
| CMAT | Coefficient of variation of LMAT | All |
| CDIV | Diversity of cover types | All |
| DEBRIS | Square root of logs, fallen trees, rocks, etc. within 3 m | All |
| SAP | Square root of sapling nos. within 3 m | A, T1, F1, S |
| TN | Square root of tree nos. within 3 m | L, A2, T, F1, S |
| TD | No. of different tree species within 3 m | All but C, L1 |
| BASAL | $Log_{10}$ total tree basal area within 3 m | All but C, A |
| BN | Square root of shrub nos. within 3 m | All but A |
| BD | Shrub species diversity within 3 m | C, T, S, F1 |
| BVL | $Log_{10}$ total shrub volume within 3 m | C, L, S, F2 |
| BVD | Shrub volume diversity | C1, L, T, S, F1 |
| AGRASS | Arc sine of the proportion of live grass cover | All but C2, F |
| ALITTER | Arc sine of the proportion of leaves, sticks, etc. cover | All but F2, S2 |
| AWOOD | Arc sine of the proportion of branch, tree, and log cover | All but C1, A2 |

[a]C, clear-cutting; A, aspen; L, lodgepole pine; T, transition forest; S, spruce; F, mature forest.

TABLE 2. Variables used for quantifying microhabitat structure in four macrohabitats in Point Pelee National Park

| Variable | Description | Plot[a] |
|---|---|---|
| Q1 | Amount of vegetation from 0 to 0.25 m | All |
| Q2 | Amount of vegetation from 0.25 to 1 m | All |
| SUMQ | Total vegetation below 1.75 m | All |
| DIV | Vegetation profile diversity | All |
| AP1 | Arc sine of the proportion of vegetation in the $0-0.25$ m layer | All |
| AP2 | Arc sine of the proportion of vegetation in the $0.25-1$ m layer | All |
| VERT | Vertical vegetation density from 1.75 m | O, S, F |
| DVERT | Vertical density diversity | All |
| LMAT | $Log_{10}$ mat depth | G, O |
| CMAT | Coefficient of variation of LMAT | All |
| TN | Square root of tree nos. within 3 m | F |
| TD | No. of different tree species | F |
| TSD | Tree species diversity | F |
| SIZD | Tree size diversity | F |
| STDEN | Square root of distance to nearest tree | All |
| SSDEN | Square root of distance to nearest sapling | G, O, F |
| SBDEN | Square root of distance to nearest shrub | G, O, F |
| BUSHN | Square root of shrub nos. within 3 m | G, O, F |

[a]G, grassland; O, old field; S, sumac; F, forest.

imize the among to within groups sums of squares from group means. I used a conservative model where discriminating variables were included in the analysis if they significantly contributed to group separation at $p < 0.05$; variables were excluded at $p > 0.025$.

## Results

### Macrohabitat selection

Do the relative abundances of temperate small mammal species depend upon macrohabitat?

Capture frequencies in the two sets of Alberta replicates revealed heterogeneity in small mammal frequencies across the six macrohabitats (Table 3). Some macrohabitat preference is obvious just by examining these frequencies. Long-tailed voles were restricted to clearcut plots whereas meadow voles occupied clear-cuttings as well as a grass covered clearing in one of the aspen plots. These observations are consistent with literature reports of habitat occupancy by these two *Microtus* species (e.g., Findley 1951; Koplin and Hoffman 1968; Radvanyi 1970, 1971; Birney et al. 1976; Kirkland 1977; Martell and Radvanyi 1977; Randall and Johnson 1979) and with their herbivorous diets. *Eutamias* was absent from the lodgepole and mature forest plots and had variable densities in the remaining macrohabitats. *Clethrionomys, Peromyscus,* and *Sorex* occupied all macrohabitats (though not all replicates), but variation in numbers among macrohabitats and among species indicated differences in macrohabitat selection. I analyzed

TABLE 3. Captures of the six most common small mammals in two replicates of six macrohabitats in the Kananaskis Valley

| Species[a] | Clear-cutting | Aspen | Lodgepole | Transition | Spruce | Forest |
|---|---|---|---|---|---|---|
| | | | First replicate | | | |
| Cg | 0(0)[b] | 6(3) | 25(8) | 27(7) | 25(9) | 24(9) |
| Ea | 8(4) | 0(0) | 0(0) | 1(1) | 56(11) | 0(0) |
| Ml | 1(1) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| Mp | 4(3) | 2(2) | 0(0) | 0(0) | 0(0) | 0(0) |
| Pm | 28(13) | 0(0) | 0(0) | 1(1) | 26(6) | 6(3) |
| S | 18(12) | 5(5) | 0(0) | 7(7) | 2(2) | 1(1) |
| | | | Second replicate | | | |
| Cg | 15(4) | 15(5) | 30(9) | 31(13) | 12(8) | 35(11) |
| Ea | 91(22) | 9(5) | 0(0) | 1(1) | 0(0) | 0(0) |
| Ml | 5(2) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| Mp | 6(4) | 0(0) | 0(0) | 0(0) | 0(0) | 0(0) |
| Pm | 17(5) | 1(1) | 4(3) | 11(5) | 4(2) | 29(9) |
| S | 1(1) | 5(5) | 2(2) | 6(6) | 0(0) | 1(1) |

[a]Cg, Clethrionomys gapperi; Ea, Eutamias amoenus; Ml, Microtus longicaudus; Mp, Microtus pennsylvanicus; Pm, Peromyscus maniculatus; S, Sorex spp.
[b]Number of different individuals in parentheses.

TABLE 4. Species–macrohabitat combinations responsible for dependence of species abundance on macrohabitat in the Kananaskis Valley (Clethrionomys, Eutamias, Peromyscus, and Sorex in two combined replicates of six macrohabitats)

| Combination deleted | Resultant $\chi^2$ | $p$ |
|---|---|---|
| Clethrionomys in clear-cuttings | 58.81 | <0.0001 |
| Sorex in aspen | 47.93 | <0.0001 |
| Sorex in transition | 31.4 | 0.002 |
| Eutamias in forest | 21.15 | 0.03 |

NOTE: Combinations are listed in order of contribution to significant $\chi^2$ (overall $\chi^2 = 90.25$; $p < 0.001$; no expected cell frequencies were less than four; 5 out of 24 were less than five).

small mammal dependence on macrohabitat after combining mammal abundances for each of the two replicates of the six different habitat types. Stepwise contingency analyses of the minimum number of Clethrionomys, Eutamias, Peromyscus, and Sorex known alive in the various habitats showed highly significant dependence of small mammal species abundance on macrohabitat (Table 4). Even so, only the rarity of Clethrionomys in clear-cuttings, the abundance of Sorex in aspen and transition forest and the absence of Eutamias in the mature forest were responsible for the dependence of species abundance on macrohabitat. These small mammals have some detectable macrohabitat differences, but over the vast majority of possible comparisons they appear independently distributed.

In Ontario, there was similar heterogeneity in small mammal numbers among macrohabitats (Table 5). All species except Microtus occurred in all four macrohabitats in both years of the study, but again, relative abundances were variable. As expected from literature reports of habitat preference in eastern North America (e.g., Eadie 1953; Getz 1960; Shure 1970; M'Closkey 1975; M'Closkey and Fieldwick 1975; Morris 1979), Microtus were plentiful in the old field and grassland, rare in the forest, and absent in the sumac.

Short-tailed shrews were excluded from the contingency analysis because trap mortalities and unmarked animals made density estimates unreliable. The stepwise analysis on rodent abundances across macrohabitats gave consistent results for

both years (Table 6). The dependence of rodent abundance upon macrohabitat was highly significant. In both years, Microtus was far more abundant in the grassland than expected if rodent abundances were independent of macrohabitat. In the field, there were significantly more Microtus than expected in 1978 and significantly fewer Peromyscus in 1979.

## Microhabitat selection

In Alberta, the macrohabitat analyses showed that species abundances were highly dependent upon macrohabitat, yet six small mammal species occurred on clear-cutting two, and three and four species combinations were common. Where several small mammal species cooccurred in the Kananaskis Valley, did they segregate on the basis of microhabitat structure? Do different temperate-zone small mammal species live in the same or different microhabitats?

Six of the Alberta plots had large enough sample sizes of at least two small mammal species for analysis of microhabitat segregation within macrohabitats by stepwise multiple discriminant functions analyses. All of the analyses resulted in highly significant microhabitat separation, and all but one species pair were also significantly different in microhabitat use (Table 7). Eutamias and Peromyscus were marginally different in habitat use in clear-cutting one, yet in the other two contrasts between these species (clear-cutting two, spruce one), they were significantly or highly significantly different in microhabitat. In Alberta, when species normally separated on the basis of macrohabitat cooccurred, macrohabitat separation was reinforced among species pairs by significantly different microhabitat use.

Small mammal species were captured in significantly different microhabitats, but the pattern of separation was inconsistent in that different variables acted as discriminators in different sites. Only two variables (DEBRIS, BVD) were significant discriminators in two or more plots. The actual separation was complex. Peromyscus occurred in areas of greater DEBRIS than did Eutamias in both clear-cuttings, and scored higher on DEBRIS than Clethrionomys in clear-cutting two; however, in transition two, Clethrionomys were captured in areas of higher DEBRIS than were Peromyscus. Micro-

TABLE 5. Captures of small mammals in equal sized plots of four macrohabitats in
Point Pelee National Park

| Species | Macrohabitat | | | |
| | Grassland | Old field | Sumac | Forest |
| --- | --- | --- | --- | --- |
| | 1978 | | | |
| *Blarina brevicauda* | 10 | 83 | 11 | 46 |
| *Microtus pennsylvanicus* | 146(97)[a] | 39(26) | 0(0) | 9(5) |
| *Peromyscus leucopus* | 18(10) | 18(11) | 124(31) | 188(59) |
| *Zapus hudsonius* | 3(3) | 6(5) | 1(1) | 5(5) |
| | 1979 | | | |
| *Blarina brevicauda* | 16 | 120 | 0 | 48 |
| *Microtus pennsylvanicus* | 233(147) | 73(30) | 0(0) | 3(2) |
| *Peromyscus leucopus* | 18(11) | 94(39) | 326(84) | 386(121) |
| *Zapus hudsonius* | 0(0) | 11(8) | 3(3) | 1(1) |

[a]Number of different individuals in parentheses.

TABLE 6. Species—macrohabitat combinations responsible for dependence of rodent abundance on macrohabitat in Point Pelee National Park

| Combination deleted | Resultant $\chi^2$ | $p$ |
| --- | --- | --- |
| | 1978 | |
| *Microtus* in grassland | 65.89 | <0.0001 |
| *Microtus* in old field | 13.66 | 0.0085 |
| Overall $\chi^2 = 160.02$; $p < 0.0001$ | | |
| | 1979 | |
| *Microtus* in grassland | 99.48 | <0.0001 |
| *Peromyscus* in old field | 10.91 | 0.028 |
| Overall $\chi^2 = 343.26$; $p < 0.0001$ | | |

NOTE: Combinations are listed in order of contribution to significant $\chi^2$ (no expected cell frequencies were less than one; 7 out of 24 were less than five).

habitat separation was real, but not easily interpretable in terms of discriminating variables.

In Ontario, species abundances also depended upon macrohabitat, yet at least three species cooccurred on each plot. Only one of the eight discriminant analyses of microhabitat differences and 7 of the 22 pairwise comparisons were nonsignificant at the 5% level (Tables 8 and 9). Six of the seven nonsignificant contrasts occurred in 1978 when overall rodent abundance was 56% that of 1979. This could be an indication of density dependent effects on microhabitat selection, yet three of those contrasts involved old field *Zapus* whose rarity may have precluded a valid representation of *Zapus* microhabitat use.

As in Alberta, discriminating variables were not constant among plots or years, and species responses to particular discriminators were plastic. In 1978 for example, *Blarina* in the forest were caught in microhabitats characterized by a higher proportion of vegetation in the 0.25—1 m layer (AP2) than were *Peromyscus*; whereas, in 1979, the trend was reversed. Similarly, *Microtus* in the old field in 1978 scored higher on AP2 than both *Blarina* and *Peromyscus*; but, in 1979 in the grassland, *Blarina* and *Peromyscus* scored higher than *Microtus*. Other repeated discriminators gave consistent relationships. *Peromyscus* were captured in areas of greater BUSHN than *Blarina* in all three cases, and *Blarina* scored higher than *Peromyscus* on both Q1 and SUMQ. LMAT was a significant discriminator in the old field (1979) and grassland (1978) and in both instances the ordering of small mammals was *Blarina* > *Microtus* > *Peromyscus*. This reaffirms my belief

that the microhabitat analysis was meaningful. *Blarina* are semifossorial, and *Microtus* construct runways in thick vegetation. The ordering of small mammals along LMAT reflects their physiological and ecological requirements.

Species relationships were more consistent on some discriminators than on others, but actual microhabitat separation varied through time and space.

## Discussion

Patterns of small mammal distribution in the Kananaskis Valley of Alberta and Point Pelee National Park in Ontario depended on both macro- and micro-habitat. Are these patterns simply ramifications of species preference, or are habitat distributions modified by species interactions? Four lines of evidence suggest that the patterning of separation was not due to species interactions. First, many of these temperate-zone small mammals are remarkably different in diet, morphology, and behaviour, and are unlikely competitors (Brown 1978). Second, in both the Kananaskis Valley and Point Pelee, macrohabitat selection was common (e.g., *Microtus* in clear-cuttings in Alberta and fields in Ontario) as was the dependence of species relative abundances on macrohabitat. This points to some form of macrohabitat preference, at least for some species. Third, microhabitat separation, though the rule, was inconsistent. Even when the same discriminating variable was responsible for species separation in more than one analysis, the ordering of species along that variable was often unpredictable. Fourth, detailed analyses of supposed competitors (*Peromyscus* and *Clethrionomys* in Alberta and *Peromyscus* and *Microtus* in Ontario) have shown that they were independently distributed within macrohabitats, and there was no indication of competitive interference (Morris 1983). Macro- and micro-habitat selection in temperate-zone small mammals appear to be a result of innate species differences in habitat preference.

My results imply that at least some subsets of macrohabitats are identified by small mammals and used in a coarse-grained manner. Inside these large-scale patches, species also appear coarse-grained with respect to microhabitat because most species pairs were to some degree significantly different in trap-revealed microhabitat use. But this does not necessarily mean that at the behavioural level animals perceive their environment as coarse grained. Fine-grained foragers will appear statistically to be coarse grained in variable environments. This is because they should restrict their actual foraging to the most

TABLE 7. Pairwise species microhabitat separation by stepwise multiple discriminant functions analyses in five plots in the Kananaskis Valley

| Plot[a] | Discriminating variables | Species pair[b] | F-ratio | p |
|---|---|---|---|---|
| C1 | DEBRIS, BVD | *Eutamias* × *Peromyscus* | 2.56 | 0.0871 |
| | | *Eutamias* × *Sorex* | 13.44 | <0.0001 |
| | | *Peromyscus* × *Sorex* ($F = 10.27$; $p < 0.0001$) | 17.07 | <0.0001 |
| C2 | DVERT, LMAT, DEBRIS | *Clethrionomys* × *Sorex* | 3.37 | 0.0210 |
| | | *Clethrionomys* × *Peromyscus* | 12.30 | <0.0001 |
| | | *Eutamias* × *Peromyscus* ($F = 6.65$; $p < 0.0001$) | 9.14 | <0.0001 |
| A2 | AWOOD | *Clethrionomys* × *Eutamias* | 9.57 | 0.0053 |
| T2 | DEBRIS, BVD, SUMQ | *Clethrionomys* × *Peromyscus* | 10.08 | <0.0001 |
| S1 | CDIV, BD | *Clethrionomys* × *Eutamias* | 4.36 | 0.0152 |
| | | *Clethrionomys* × *Peromyscus* | 3.98 | 0.0216 |
| | | *Eutamias* × *Peromyscus* ($F = 5.01$; $p = 0.0007$) | 6.34 | 0.0025 |
| F2 | CMAT, BASAL | *Clethrionomys* × *Peromyscus* | 14.26 | <0.0001 |

[a]C, clear-cutting; A, aspen; T, transition forest; S, spruce; F, mature forest.
[b]When more than two species were contrasted, the overall F and its probability are given in parentheses.

TABLE 8. Species microhabitat separation by stepwise multiple discriminant functions analyses in four macrohabitats in Point Pelee National Park

| Sample sizes[a] | | | | Habitat[b] | Year | F-ratio | Significant variables[c] |
|---|---|---|---|---|---|---|---|
| *Bb* | *Mp* | *Pl* | *Zh* | | | | |
| 46 | — | 188 | — | F | 1978 | 11.28** | SIZD, AP2, DIV |
| 48 | — | 386 | — | F | 1979 | 15.74** | Q1, BUSHN, CMAT, TN, AP2 |
| 11 | — | 124 | — | S | 1978 | No separation | |
| 10 | — | 326 | — | S | 1979 | 10.67** | SUMQ, BUSHN |
| 83 | 39 | 18 | 6 | O | 1978 | 3.39* | Q1, AP2 |
| 120 | 73 | 94 | 11 | O | 1979 | 7.16** | BUSHN, STDEN, LMAT, VERT |
| 10 | 142 | 18 | — | G | 1978 | 14.56** | LMAT, SUMQ |
| 16 | 233 | 18 | — | G | 1979 | 7.20** | AP2, SBDEN |

NOTE: *, $0.01 < p < 0.05$; **, $p < 0.001$.
[a]Total captures in the 135 stations in each macrohabitat; only species included in the appropriate analysis are reported. *Bb*, *Blarina brevicauda*; *Mp*, *Microtus pennsylvanicus*; *Pl*, *Peromyscus leucopus*; *Zh*, *Zapus hudsonius*.
[b]F, forest; G, grassland; O, old field; S, sumac.
[c]Listed in order of importance to species separation.

rewarding "patches," yet to get to those patches they must travel through less productive areas where their optimal strategy is not to forage (Rosenzweig 1974, 1981). If individuals are "trappable" in all microhabitats, (and "poor" patches are not much greater in size than "good" patches) then statistically we expect to record most captures in profitable patches where animals are foraging. Trap-revealed microhabitat use of these fine-grained searchers will be indistinguishable from that of coarse-grained forms which are occasional occupants of suboptimal locations.

At the statistical or distributional level of enquiry this is not a problem. Our interest is properly focused on whether or not species are subdividing habitat. The answer for temperate-zone small mammals is an unequivocal yes. But if our goal is to understand how and why these exploitation differences have evolved, we will need data on actual foraging patterns in different sized patches of variable rewards.

Are the macrohabitat and microhabitat patterns really different, or are they in some way part of the same process? Do the patterns of microhabitat use lead to those at the macrohabitat level?

For reasonably small animals of intermediate mobility like small mammals, this is quite plausible. In the Kananaskis Valley, my macrohabitat designations were arbitrary and actual plots were selected on the basis of vegetation homogeneity. Even though each plot was distinct and homogeneous, with the exception of clear-cuttings, macrohabitats graded one into another. If I were to walk a transect across the valley I could identify many stations as belonging to my various macrohabitat categories, yet many others would in some way be intermediate. I am willing to concede that small mammals are better discriminators of habitat than I, but even they are unlikely to make sharper distinctions along continuously distributed microhabitat variables than I or my computer. Then why are there two apparent levels of habitat preference?

In Point Pelee, the answer may be simple. Macrohabitats

TABLE 9. Minimal pairwise species microhabitat separation by stepwise multiple discriminant functions analyses in four macrohabitats in Point Pelee National Park

| Habitat | Species pair | 1978 | | 1979 | |
|---|---|---|---|---|---|
| | | $F$-ratio | $p$ | $F$-ratio | $p$ |
| Forest | Blarina × Peromyscus | 11.28 | <0.0001 | 15.74 | <0.0001 |
| Sumac | Blarina × Peromyscus | No separation | | 10.67 | <0.0001 |
| Old field | Blarina × Microtus | 5.53 | 0.0048 | 3.42 | 0.0016 |
| | Blarina × Peromyscus | 1.96 | 0.1452 | 12.53 | <0.0001 |
| | Blarina × Zapus | 1.50 | 0.2272 | 3.30 | 0.0021 |
| | Microtus × Peromyscus | 6.31 | 0.0024 | 15.62 | <0.0001 |
| | Microtus × Zapus | 2.97 | 0.0544 | 3.06 | 0.0040 |
| | Peromyscus × Zapus | 0.20 | 0.8166 | 2.21 | 0.0338 |
| Grassland | Blarina × Microtus | 2.13 | 0.1217 | 1.94 | 0.1454 |
| | Blarina × Peromyscus | 11.22 | <0.0001 | 7.85 | 0.0005 |
| | Microtus × Peromyscus | 28.91 | <0.0001 | 12.55 | <0.0001 |

NOTE: Pairwise separation is represented by the $F$-ratios extracted from the group separation matrices of the multispecies comparisions reported in Table 8.

were clearly defined by sharp ecotones along the old field and grassland.

In the Kananaskis and in most natural landscapes where habitat boundaries are not discrete, the answer probably lies in the patchy distribution of the animals themselves. Even with only one replicate plot of each of the six macrohabitats, the patchiness of small mammal distribution was apparent. *Clethrionomys* occurred in one clear-cutting and not another, *Peromyscus* occurred in one lodgepole plot and not another, and *Eutamias* occurred in one aspen and one spruce but not their replicates. Macrohabitat effects related to species presence or absence, in part, seem to reflect unequal accessibility among macrohabitat patches.

Macrohabitat effects related to variation in relative abundances of constituent species probably mirror microhabitat variability, resource abundance levels and species interactions. Optimality models of microhabitat use will likely give a good fit to actual species abundance patterns as long as they are overlaid with a suitable framework expressing probabilities of local colonization and extinction.

The dependence of species relative abundances on macrohabitat means that at the most fundamental level field ecologists should be extraordinarily cautious if they are considering pooling resource use data across habitat types. At the very least, they should analyze for macrohabitat effects as I have done here. In addition to species preferences, it is uncommon to find homogeneous variable sets across macrohabitats (Morris 1980). Indeed, if we accept a statistical definition of macrohabitat as a homogeneous process of microhabitat variation, then it is clearly improper to analyze microhabitat preference across macrohabitat boundaries. Failure to disentangle macro- and micro-habitat effects can result in neat habitat utilization patterns that are more fictitious than real.

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