

## Microhabitat preferences of two species of deermice *Peromyscus* in a northeastern United States deciduous hardwood forest

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Differences in microhabitat utilization by two sympatric species of deermice, *Peromyscus leucopus* and *P. maniculatus* were assessed in deciduous hardwood forest. In the initial descriptive experiment, a series of 12 parameters were measured for 1 m<sup>2</sup> areas around live-trap stations. Four subsequent experimental tests involved placing live-traps at specified locations with respect to logs, plant cover above the trap, the base of trees of different sizes, and on trunks of trees of different types and sizes. *P. leucopus* were caught more often than expected with (1) more plant cover directly above the trap, (2) at the sides of large logs, (3) at the base of medium-to-large sized trees, and (4) on the sides of large oak and sugar maple trees. *P. maniculatus* were captured more often than expected with (1) at the base of large diameter trees, and (2) on the sides of large beech and sugar maple trees. Mice of both species exhibited similar preferences for some habitat features, including distance from the trap to the nearest tree and amount of herbaceous ground cover around the trap. They differed with respect to many of the habitat features tested, including, diameter of the nearest tree, amount of cover above the trap, and the nature of the ground cover near the trap. These findings suggest ways in which the species differ in microhabitat utilization and further our understanding of the degree of specialization for each species.

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### Introduction

Investigators exploring habitat distributions of various species of North American woodland rodents (e.g., Jameson 1949, Linduska 1950, Morris 1979, Dueser and Hallett 1980, Drickamer 1987a), have posed questions pertaining to macrohabitat relationships, microhabitat relationships, and range overlap with possible competitive exclusion. Though a variety of species have been investigated, one genus, *Peromyscus*, has received more attention than any other taxon. Two species, *Peromyscus leucopus* (Rafinesque, 1818) and *P. maniculatus* (Wagner, 1845), have been the subjects of a considerable portion of these investigations.

By macrohabitat features I mean here those general characteristics of the physical and living environment such as forest type, elevation, degree of human disturbance, etc. Results of macrohabitat studies differ regarding the habitat relationships of the two species of deermice even within same general region of North America. In central New York state, Klein (1960) reported *P. maniculatus* preferred forest stands of black maple and birch, whereas *P. leucopus* were captured most frequently in areas

dominated by oak, though the latter species did not exhibit any strong overall habitat preference and was thus more of a generalist. In southeastern Ontario, Smith and Speller (1970) reported *P. maniculatus* was more of a generalist, being recorded in all forest types, whereas *P. leucopus* were restricted to upland hardwood forests. In western Massachusetts, I found that *P. leucopus* were captured in a wide variety of forest types, including all successional stages (Drickamer 1987a). In the same forest, *P. maniculatus* were restricted to the late successional climax areas.

Several previous investigators have studied the distributions of the two species of deermice with respect to particular microhabitat features. By microhabitat features I mean here such characteristics as the herbaceous vegetation density and composition (M'Closkey and Lajoie 1975), physical factors (Jameson 1949), social influences (M'Closkey and Fieldwick 1975), and the availability of refuges (Bendell 1961). Dueser and Shugart (1978) studied the relationships between small forest mammals and a series of 29 microhabitat variables in eastern Tennessee. The abundance of *P. leucopus* was positively related to the diversity of woody species, the dispersion of the understory and overstory, compactability of the soil and litter layer, and the size of available tree stumps and negatively related to the evergreen component of both understory and overstory, and the thickness of the woody vegetation. Morris (1979), reported that the two species selected different habitats based upon the amount of leaf litter, the basal area of trees present, and the total amount of vegetation. Morris (1979) also reported a high negative relationship between mice of the two species, similar to that which I subsequently reported for the same two species in New England (Drickamer 1987a).

The purpose of the experiments presented here was to test, both descriptively and experimentally, aspects of the microhabitat utilization of two species of deermice, *P. leucopus* (subspecies *noveboracensis*) and *P. maniculatus* (subspecies *gracilis*). The results are important with regard to questions of niche breadth of the two species and to longer term issues in applied biogeography with respect to our ability to assess the effects of human interference or habitat disturbance on distributions of indicator species such as deermice. *Peromyscus* are widespread and occupy a variety of habitats; they are becoming increasingly important with regard to monitoring environmental and habitat changes. It is thus important now to begin to obtain useful data on their habitat utilization and degree of specialization to provide baseline data for future comparisons. The initial experiment, a descriptive study of capture rates of the mice in relation to 12 parameters measured for each trap station, was designed to assess which of a series of microhabitat characteristics might be important to one or both species. It was followed by four experiments in which live-traps were placed in specific locations to test particular hypotheses about capture rates in relation to logs, plant cover above the trap, attraction to trees of different sizes, and use of the trunks of trees of various species and sizes. Though there is some congruence between the parameters measured in the initial unmanipulated test and the experiments that follow in terms of the microhabitat parameters measured, the latter were not specifically designed as

follow-up tests, but rather provided additional information on the degree of habitat generalization or specialization by mice of the two species.

### Study site

The investigations were conducted in the Hopkins Memorial Forest, located in Williamstown, Massachusetts, U.S.A. (42°30' N, 73°15' W). Elevations in the forest range from 200 to 730 m. The forest covers an area of over 850 ha and contains the entire Birch Brook watershed with many ridges and valleys. As the result of variations in past land-use history, the forest contains a diversity of ecological communities in varying seral stages. These include several open fields, fields with alder *Alnus* spp. thickets, and stand of various tree species (percentage of total basal area calculated from diameter at breast height data for each species given in parentheses): red oak *Quercus rubra* (22%), red maple *Acer rubrum* (16%), sugar maple *Acer saccharum* (15%), American beech *Fagus grandifolia* (15%), white birch *Betula papyrifera* (15%), grey birch *Betula lenta* (4%); American ash *Fraxinus americana* (4%), yellow birch *Betula lutea* (3%), striped maple *Acer pennsylvanicum* (1%), hophornbeam *Ostrya* spp. (1%), and juneberry *Amelanchier* spp. (1%).

### Methods

The entire Hopkins Memorial Forest is mapped with a series of surveyed cruise lines running east-west at intervals of 200 m and plot lines running north-south at intervals of 100 m, making a rectangular grid with plots of about 2 ha. These grid squares serve as the basis for vegetation surveys of the forest and for selecting particular sites for trapping rodents.

In each of the experiments, folding aluminum live-traps (H. B. Sherman Co., Tallahassee, Florida, U.S.A.) were placed in specified locations based upon the forest grid system. The traps remained open for 3 days in each experiment. All mice caught were marked with a toe-clip and ear-punch system and released immediately at the site of capture. During the course of these experiments, 87 mice were recaptured; data from these mice were excluded from the analyses. Two species of *Peromyscus* inhabit the Hopkins Memorial Forest, *Peromyscus maniculatus gracilis* (called *P. maniculatus* hereafter) and *Peromyscus leucopus noveboracensis* (called *P. leucopus* hereafter). Mice were identified according to the criteria of Hall (1981), Choate (1973), and Feldhamer *et al.* (1983). The sex and age (pelage was used to distinguish adults from juveniles) of each mouse were also recorded; since no differences were noted, from preliminary analyses, for any of the experimental tests, the data were lumped with regard to age and sex for all analyses. In order to avoid possible seasonal shifts in habitat preferences by the mice, I trapped only during the summer months, from June through August.

There are over four hundred 2-ha plots (each plot is considered a grid location) available for trapping in the Hopkins Memorial Forest. For purposes of the present study I selected 100 different grid locations based on a previous study in the forest (Drickamer 1987a) to insure that there be mice of both species present at most if not all locations. Twenty grid locations were used for each of the five separate experiments. Of the 100 locations used, 93 produced at least one mouse of each species, five had only *P. leucopus* and two had only *P. maniculatus*. As detailed in the Results, sufficient numbers of both species were caught for each of the five experiments to permit valid analyses and interpretation of the microhabitat responses of the mice.

### Experiment I – Multiple variables

The purpose of the first experiment was to test responses to 12 different microhabitat variables to determine which were important to the mice. Twenty 1-ha plots were trapped for three days each with 100 live-traps arranged in a 10 m × 10 m grid; one trap was placed at each station (total of 300 trap nights at each grid location). The traps were placed exactly at a grid station without reference to any particular habitat features. Each trap site was measured with respect to 12 variables: (1) percentage slope of the ground under

the trap; (2) distance (m) to the nearest tree of at least 2.5 cm diameter at breast height; (3) diameter of the nearest tree or shrub (cm) of at least 2.5 cm diameter at breast height; (4) percentage cover above the trap from the ground to 25 cm above the ground; (5) percentage cover above the trap from the ground to 1.5 m above the ground; (6) percentage cover above the trap from the ground to 2 m above the ground; and the following variables measured in a 1 m square centered around the trap, (7) percentage of area occupied by stems from trees and shrubs; (8) percentage of bare ground; (9) percentage of herbaceous ground cover; (10) percentage of log material  $\geq 2.5$  cm as ground cover; (11) % rock exposure as ground surface; and (12) % leaf litter as ground cover. For variables 5–12 a 1-m square frame, divided into 100 10-cm by 10-cm squares by a network of strings, was used to estimate the percentages. Data were analyzed using t-tests and Chi-square goodness-of-fit and contingency tests (Sokal and Rohlf 1981).

#### Experiment II – Trapping near logs

This experiment was designed to determine whether logs lying on the floor would affect the capture rates for mice of either species. Twenty 1-ha plots were trapped for 3 nights each. Within each plot 100 live-traps were arranged in a  $10 \times 10$  grid with the trap at each station placed as near to the grid point as possible, but in 1 of the following 4 types of locations: (1) next to and parallel with a log of  $\geq 25$  cm diameter; (2) on top of a log  $\geq 25$  cm diameter; (3) next to and parallel with a log of  $10 \text{ cm} \leq x < 25 \text{ cm}$ ; or (4) on top of a log of  $10 \text{ cm} \leq x < 25 \text{ cm}$ . For each grid of 100 stations, 25 traps were placed at each of the 4 specified location types. The data were analyzed using Chi-square goodness-of-fit and contingency tests.

#### Experiment III – % cover above trap

This experiment was designed to determine whether amounts of herbaceous plant cover up to 1 m above the trap would affect the capture frequencies for the two species. Twenty 1-ha plots were trapped for 3 nights each. On each plot, 100 live-traps were arranged in a  $10 \times 10$  grid. Each trap was placed within 1 m of the grid site, in a location that would match 1 of 5 designated densities of overhead cover to a height of 1 m: (1) 0–10%; (2) 20–30%; (3) 45–55%; (4) 70–80%; or (5) 90–100%. Traps were positioned in a grid such that no more than two adjacent trap stations in any direction were placed by trees of the same dbh. The data were analyzed using Chi-square goodness-of-fit and contingency tests.

#### Experiment IV – Tree size – trapping at base of tree

This experiment was designed to assess whether capture rates would vary at the base of trees of varying diameter-at-breast-height (dbh). Twenty 1-ha plots were trapped for 3 nights each. On each plot, 100 live-traps were arranged in a  $10 \times 10$  grid. Each trap was placed within 2.5 m of the grid site, in a location that would match 1 of 5 designated (dbh) measurements: (1)  $0 \text{ cm} < \text{dbh} \leq 2.5 \text{ cm}$ ; (2)  $2.5 \text{ cm} < \text{dbh} \leq 7.5 \text{ cm}$ ; (3)  $7.5 \text{ cm} < \text{dbh} \leq 15 \text{ cm}$ ; (4)  $15 \text{ cm} \leq \text{dbh} < 25 \text{ cm}$ ; (5)  $\text{dbh} \geq 25 \text{ cm}$ . Traps were positioned in a grid such that no more than two adjacent trap stations in any direction were placed by trees of the same dbh. The data were analyzed using Chi-square goodness-of-fit and contingency tests.

#### Experiment V – Trees – use of 3rd dimension

The final experiment was designed to test tendencies of the mice to climb trees of different types and sizes. Twenty 1-ha plots were trapped with 100 live-traps each. The traps were positioned on the sides of trees with 16 gauge steel wire holding the trap bottom flat against the trunk of the tree at 1.5–2 m above the ground and with the open end of the live-trap facing upward. Thus mice that were caught in these traps would have been at least as high on the tree trunk as the position of the trap. Of the 20 grids trapped, there were some where the major tree type (75% or more of the total basal area) was *Betula papyrifera* ( $n=2$ ); some with a predominance of *Acer rubrum* ( $n=3$ ), some with a predominance of a combination of *Betula papyrifera* and *Acer rubrum* ( $n=3$ ); some where the major tree type was *Quercus rubra* ( $n=5$ ); some with a predominance of *Acer saccharum* ( $n=3$ ); some with a predominance of *Fagus grandifolia* ( $n=2$ ); and some where a combination of *Acer saccharum* and *Fagus grandifolia* met the 75% total basal area criterion. Within

a grid of 100 traps located in one of the foregoing forest types, the traps were placed on equal mixtures of trees of three size categories: (1)  $5 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$ ; (2)  $10 \text{ cm} \leq \text{dbh} < 25 \text{ cm}$ ; or (3)  $\text{dbh} \geq 25 \text{ cm}$ . Also, within a trap grid, no two traps were positioned on trees that were within 5 m of one another. Overall, the 2,000 traps (20 grids  $\times$  100 traps/grid) were allocated to tree types and tree sizes such that there were 132 to 136 traps tested for each of the 15 categories created by the 5 tree types and 3 tree sizes. I assumed from this relative even pattern of trap allocation that there would not be any differential capture frequencies due to the way the traps were placed.

## Results

Across all of the experiments, a total of 1692 *P. leucopus* and 994 *P. maniculatus* were trapped, giving a grand total of 2596 mouse captures and a return of 8.7%. This return rate is comparable to other data I have obtained in the same forest (Drickamer 1987a) and is also similar to trapping rates reported from other locations for these two species (Jameson 1949, M'Closkey and Fieldwick 1975). In addition to *Peromyscus*, I captured 236 chipmunks *Tamias striatus*, 86 redbacked voles *Clethrionomys gapperi*, 27 woodland jumping mice *Napeozapus hudsonicus*, and 51 short-tailed shrews *Blarina brevicauda*.

### Experiment I

The results (Table 1) of the initial trapping involved captures of 346 *P. leucopus* and 172 *P. maniculatus*. Multiple t-tests (Sokal and Rohlf 1981) were used to analyze these results because the variable scales for the various independent variables were so different, precluding the use of ANOVA or other statistical techniques. Each independent variable was continuously distributed and in a fashion not different from the normal distribution. Because the use of multiple t-tests could increase the possibility of Type II error, I elected to reduce the alpha level for rejection of the null hypothesis to 0.02 for all tests using this data set. In Table 1, the total values for the last six independent measures, all pertaining to ground cover, exceed 100.0% due to rounding errors.

Relative to the mean values for all trap sites, *P. leucopus* were caught frequently closer to the base of the nearest tree, near larger diameter trees, with more cover above the trap at all three levels tested, and with more woody material as ground cover. They were caught less than the average for all sites with respect to distance to the nearest tree and the amount of leaf litter ground cover.

Relative to the mean values for all trap sites, *P. maniculatus* were caught more frequently on steeper slopes, near larger diameter trees, and at sites with more woody stems. They were caught less than the average for distance to the nearest tree, with regard to cover above the trap to 1.5 m, and where sites had low amounts of exposed rock and bare soil.

When the two species were compared, they differed on 10 of the 12 variables measured; they did not differ with regard to the distance to the nearest tree and the amount of herbaceous ground cover near the trap. For one variable, diameter of the

Table 1. Captures of two species of *Peromyscus* at live traps relative to 12 parameters measured at each trap sites. To obtain these data, 201-ha grids with 100 traps/grid were each live-trapped for three consecutive nights (6000 trap nights). Column (1) contains a mean ( $\pm 1$  SE) for each parameter across all 2000 trap sites. Column (2) contains mean values ( $\pm 1$  SE) for sites where *P. leucopus* were trapped, followed by (3) a t-test comparing the species mean with the mean from all sites and associated probability (4). Column (5) contains mean values ( $\pm 1$  SE) for sites where *P. maniculatus* were trapped, followed by (6) a t-test comparing the species mean with the mean from all sites and associated probability (7). Column (8) is a t-test comparing the mean values for two species, followed by the associated probability (9). Alpha = 0.02 throughout; see text for explanation.

Parameter	(1) All sites	(2) <i>P. leucopus</i>	(3) t-test vs (1)	(4) Prob.	(5) <i>P. maniculatus</i>	(6) t-test vs (1)	(7) Prob.	(8) Two species t-test	(9) Prob.
Slope (%)	6.9 (0.1)	6.4 (0.2)	1.17	ns	8.4 (0.3)	2.96	<0.01	3.78	<0.001
Distance to nearest tree (m)	2.6 (0.1)	1.7 (0.2)	3.17	<0.01	1.9 (0.2)	2.68	<0.01	0.63	ns
Diameter of nearest tree (cm)	10.8 (0.1)	14.5 (0.4)	3.92	<0.001	17.6 (0.5)	9.16	<0.001	3.14	<0.001
Cover to 10 cm above trap (%)	22.8 (1.9)	32.1 (2.1)	11.71	<0.001	19.6 (1.8)	0.86	ns	14.16	<0.001
Cover to 1.5 m above trap (%)	34.3 (2.7)	44.4 (2.9)	8.64	<0.001	28.7 (1.9)	2.57	<0.02	13.92	<0.001
Overhead canopy (%)	58.1 (2.9)	71.3 (3.1)	3.94	<0.001	57.9 (2.1)	0.17	ns	7.44	<0.001
Woody ground cover (%)	8.0 (0.2)	12.3 (0.6)	2.46	<0.02	8.8 (0.4)	0.11	ns	3.17	<0.01
Woody stems (%)	2.4 (0.1)	1.7 (0.1)	2.28	ns	3.3 (0.2)	2.97	<0.01	8.64	<0.001
Herbaceous ground cover (%)	18.1 (1.3)	20.4 (1.7)	0.67	ns	16.6 (0.9)	1.46	ns	0.77	ns
Exposed rock (%)	2.0 (0.1)	1.9 (0.1)	0.87	ns	1.0 (0.1)	2.76	<0.01	3.86	<0.001
Leaf litter ground cover (%)	16.4 (2.9)	58.1 (2.1)	9.63	<0.001	69.0 (2.4)	0.46	ns	6.97	<0.001
Bare soil exposed (%)	6.5 (0.2)	7.3 (0.2)	0.31	ns	3.9 (0.1)	3.16	<0.01	5.63	<0.001

nearest tree, both species were caught at larger trees, but the figure for *P. maniculatus* was significantly larger than for *P. leucopus*. *P. maniculatus* were caught more often at steeper slopes than *P. leucopus*. *P. leucopus* were caught more often than *P. maniculatus* with more cover at all three levels measured. With respect to ground cover, *P. leucopus* were trapped more frequently with more woody material, more exposed rock, and more bare soil, while, *P. maniculatus* were trapped more often with more woody stems site and more leaf litter near the trap.

#### Experiment II

The results (Table 2) of tests using traps placed beside or on top of logs to different diameters indicated that there were significant deviations from the expected patterns for one species, but not the other. A total of 376 *P. leucopus* and 172 *P. maniculatus* were captured on the 20 grids. For *P. leucopus*, both the size of the log and the trap location were important. Mice were caught more often than expected near or on top of large logs compared to small logs and they were caught more often beside logs than on top. For *P. maniculatus* there were no significant deviations from expected frequencies of captures, either according to the size of the log or the trap location.

#### Experiment III

The results (Table 3) of tests involving placement of traps in specific locations with designated amounts of overhead cover to 1 m above the trap, indicated significant variation for *P. leucopus*, but not *P. maniculatus*. A total of 220 *P. leucopus* and 129 *P. maniculatus* were captured. *P. leucopus* were caught more often than expected at high levels of overhead cover and less often than expected with low levels of cover. There were no significant deviations from the expected values for *P. maniculatus*.

#### Experiment IV

The results (Table 4) of tests involving placement of traps at the base of trees with various dbh measurements resulted in significant variation within each species. A total of 533 *P. leucopus* and 407 *P. maniculatus* were captured. Both *P. leucopus* and *P. maniculatus* were caught more often than expected at larger dbh trees and less often at smaller dbh trees. The contingency analysis of species-by-tree-size capture frequencies was not statistically significant.

#### Experiment V

A total of 167 *P. leucopus* and 124 *P. maniculatus* were captured. For both species, the captures of mice at *Betula papyrifera* and *Acer rubrum* were small enough to require combining these two tree types to avoid problems with too many cells in the analysis with low expected values. Analyses of the data for *P. leucopus* (Table 5) revealed significant variation in capture rates with respect to both tree type and tree size; the contingency analysis was not significant. For tree type, more *P. leucopus* were caught at *Acer saccharum*, *Quercus rubra*, and *Fagus grandifolia* and fewer at *A. rubrum* and

Table 2. Number of captures of two species of deermice with respect to trap placement next to or on top of logs in two sizes. Small logs were 10 cm < x < 25 cm and large were > 25 cm.

Position	Log size		Statistics
	Small	Large	
<i>Peromyscus leucopus</i>			
Top	62	107	Size $\chi^2 = 34.56$ ; <i>d.f.</i> = 1; <i>p</i> < 0.001
Side	69	138	Position $\chi^2 = 3.84$ ; <i>d.f.</i> = 1; <i>p</i> < 0.050
<i>Peromyscus maniculatus</i>			
Top	48	39	Size $\chi^2 = 0.21$ ; <i>d.f.</i> = 1; <i>p</i> > 0.20
Side	41	44	Position $\chi^2 = 0.02$ ; <i>d.f.</i> = 1; <i>p</i> > 0.20

Table 3. Frequencies of captures of *P. leucopus* and *P. maniculatus* in live-traps under five different conditions of herbaceous plant cover at 1 m above trap. Twenty 1 ha plots were trapped with 100 traps per grid. Expected values from a Chi-square contingency analysis are provided in parentheses.

% cover at 1 m	<i>P. leucopus</i>	<i>P. maniculatus</i>
0 – 10%	21 (31)	28 (18)
20 – 30%	31 (35)	25 (21)
45 – 55%	43 (43)	26 (26)
70 – 80%	61 (52)	21 (30)
90 – 100%	64 (59)	29 (34)
$\chi^2 =$	31.54	1.50
<i>d.f.</i> =	4	4
<i>p</i>	< 0.01	> 0.20

Table 4. Frequencies of captures of *P. leucopus* and *P. maniculatus* in traps placed at the base of trees of five different categories of diameter-at-breast-height. Twenty 1 ha grids were trapped with 100 traps per grid. Expected values from a Chi-square contingency analysis are provided in parentheses.

Tree size (dbh)	<i>P. leucopus</i>	<i>P. maniculatus</i>
0 cm ≤ dbh ≤ 2.5 cm	74 (84)	75 (65)
2.5 cm < dbh ≤ 7.5 cm	99 (89)	58 (68)
7.5 cm < dbh ≤ 15 cm	86 (94)	79 (71)
15 cm < dbh ≤ 25 cm	121 (116)	84 (89)
dbh > 25 cm	153 (150)	111 (114)
$\chi^2 =$	36.49	18.24
<i>d.f.</i> =	4	4
<i>p</i>	< 0.001	< 0.001



Table 5. Capture frequencies at traps placed 1.5–2 m above the ground attached to the sides of tree of various types and of various diameter-at-breast-height measurements. Twenty grids were trapped with 100 traps per grid. The expected values from the Chi-square contingency analysis are provided in parentheses.

Tree type	5 cm ≤ dbh < 10 cm	10 cm ≤ dbh < 25 cm	dbh ≥ 25 cm
<i>P. leucopus</i>			
<i>Betula papyrifera</i> and <i>Acer rubrum</i>	5 (6)	12 (14)	24 (21)
<i>Acer saccharum</i>	7 (7)	17 (17)	26 (26)
<i>Fagus grandifolia</i>	5 (4)	14 (10)	9 (14)
<i>Quercus rubra</i>	7 (7)	14 (16)	27 (25)
Tree size $\chi^2 = 34.55$ ; <i>d.f.</i> = 2; $p < 0.001$ Tree type $\chi^2 = 28.84$ ; <i>d.f.</i> = 3; $p < 0.001$ Contingency $\chi^2 = 4.92$ ; <i>d.f.</i> = 6; $p > 0.05$			
<i>P. maniculatus</i>			
<i>Betula papyrifera</i> and <i>Acer rubrum</i>	2 (2)	3 (3)	5 (5)
<i>Acer saccharum</i>	5 (5)	11 (10)	18 (19)
<i>Fagus grandifolia</i>	7 (7)	14 (13)	22 (23)
<i>Quercus rubra</i>	4 (4)	7 (8)	16 (15)
Tree size $\chi^2 = 25.74$ ; <i>d.f.</i> = 2; $p < 0.001$ Tree type $\chi^2 = 52.75$ ; <i>d.f.</i> = 3; $p < 0.001$ Contingency $\chi^2 = 0.47$ ; <i>d.f.</i> = 6; $p > 0.05$			

*Betula papyrifera* than expected. For tree size, more *P. leucopus* were captured at large trees and fewer at small trees than expected.

For *P. maniculatus* (Table 5), the analyses revealed significant deviations from expected values for both tree type and tree size; the contingency test was not statistically significant. More mice than expected were captured near *A. saccharum* and *F. grandifolia* and fewer near the other three tree species. With respect to tree size, more mice than expected were captured at large trees and fewer at small trees than expected.

### Discussion

From the foregoing experiments and analyses it is evident that mice of the two species, *P. leucopus* and *P. maniculatus*, respond differently to particular aspects of the microhabitat. Perhaps the most striking difference is with respect to vegetation cover above the trap. It should be noted that the three measures used in Experiment I are not entirely independent of one another, but since they do permit the examination of whether cover at different heights is important to the mice, I have proceeded. *P. leucopus* were found more often with significant amounts of plant cover above the trap (Experiment I), whereas *P. maniculatus* were generally not affected by the amount of plant cover. Further, in a direct experimental test (Experiment III), *P. leucopus* selected traps with higher amounts of plant cover at 1 m above the trap and *P. maniculatus* were not affected. The difference in microhabitat preference exhibited

here with respect to vegetation cover may be related to the finding reported earlier that *P. leucopus* are more active on cloudy nights and *P. maniculatus* on clear nights (Drickamer and Capone 1977). There apparently are activity differences between the species based upon the degree of exposure to the night sky from above.

Mice of both species climb trees with diameters at breast height of >25 cm and both are caught more often in traps placed at the base of trees with diameters of >25 cm, though *P. leucopus* were also captured in significant numbers at trees of intermediate diameters ( $15 \text{ cm} < \text{dbh} \leq 25 \text{ cm}$ ) (Experiment IV). The species differ in terms of the utilization of the third dimension for trees of different types (Experiment V); *P. leucopus* utilize oak and sugar maple more, whereas *P. maniculatus* prefer beech and sugar maple. This last finding is in agreement with what I reported earlier concerning the macrohabitat preference of *P. maniculatus* for late successional forest and *P. leucopus* being a bit broader in selection of general forest type (Drickamer 1987a). While both species utilize fallen logs in the course of their nightly travels, *P. leucopus* apparently prefer to travel along paths that utilize the sides of large logs, whereas *P. maniculatus* do not exhibit any differential activity concerning log size or location (Experiment II).

Together, these data on microhabitat utilization bear on two issues, competition and niche breadth. The present data, in conjunction with earlier information on these two species concerning macrohabitat, daily activity (Drickamer 1987b), and recruitment, suggest that any competition between these two species of *Peromyscus* may be minimized via a variety of differences in the niches occupied by mice of the two taxa. The two species apparently are more active in different portions of the physical/living environment (Drickamer 1987a), they are active at different times of the day (Drickamer 1987b), and they have different annual patterns of recruitment (Drickamer 1978). Examination of the present data set does not indicate that either species has a particularly wider or narrower niche than the other for the range of parameters tested; both species appear capable of utilizing a wide range of microhabitats. It would be interesting to test the possible species flexibility with regard to niche breadth by removing each species in separate areas where both are normally present to determine whether this manipulation resulted in a change in the utilized niche for the remaining species.

*P. leucopus* and *P. maniculatus* have been co-existing for many decades in the area of range overlap extending from southern Ontario, Canada northeastward throughout much of New England in the United States and southeastern Canada. Whether the microhabitat differences observed in the present study and similar endeavors (Jameson 1949, Klein 1960, M'Closkey and Lajoie 1975, Dueser and Shugart 1978, Drickamer 1987a), testing both macrohabitat and microhabitat characteristics, are due to a long history of co-existence or to a more recent overlap resulting from range extension by one or both species is difficult to ascertain. What is evident, when we examine the relatively static distribution picture existing for the past several decades, is that there are a variety of critical parameters on which these two species differ, including

seasonality of recruitment, activity differences under varying weather conditions, time of night when they are most active, macrohabitat selection, and a series of microhabitat features.

The findings from the present study as well as some of the methods could have important implications for the study of applied biogeography. Knowledge about the habitat preference of particular species and about their relationships with particular characteristics of the habitat may serve as guideposts for monitoring any changes in their presence or abundance. By knowing what habitat features to examine we can ascertain what, if any, are the consequences of habitat disturbance for the mice. *Peromyscus* of the two taxa studied here are rather plentiful and not in danger with regard to extinction. However, for many other mammalian species that are threatened or endangered, the types of investigations that have been conducted here on two species of deermice may prove to be a useful model for exploring critical habitat features. In many instances it may be that particular microhabitat features are of critical importance to the continued survival and reproduction of a species. Knowledge gained concerning both the techniques and the biology of the mice may be of broader relevance with regard to mammalian species, particularly rodents, that are currently threatened or endangered.

Two final points are worth noting. First, a key technique for future studies of differential habitat selection in small rodents is the use of experimental manipulation. Manipulation can be of two types, either the purposeful placement of traps or nest boxes with respect to particular features of the habitat, or the direct manipulation of the habitat. The former technique was used in the present sequence of experiments. A good example of the latter technique involves the creation of designated microhabitats through the use of artificial branches (shrubs) placed in different directions for *P. leucopus* (M'Closkey 1976). Second, throughout virtually all of the studies that have been conducted to date concerning habitat selection in *Peromyscus* and other small rodents, a clear and consistent assumption has been that the capture frequencies of mice relate directly to the proportional utilization of particular habitat types or subareas within a habitat. While I have no basis for challenging this assumption, it would be important, at some time, to check on the reliability of the assumption through other techniques, e.g., radio-tracking, powder-tracking, or direct observation. Such data have been reported connecting foraging activity and microhabitat preferences in heteromyid rodents (Price 1977), but further analyses testing our assumption regarding trapping and levels of activity in the habitat are needed.

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