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Microhabitat Separation among Sympatric Microtines, Clethrionomys californicus, Microtus oregoni and M. richardsoni

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ABSTRACT: This study examined microhabitat distribution of *Microtus oregoni*, *M richardsoni* and *Clethrionomys californicus*, sympatric microtine rodents that are similar in morphology and life history patterns. Populations were sampled in riparian and upland habitats within old-growth and mature forest stands in the western Cascade Range of Oregon. As indicated by discriminant function analysis, relative to availability *C. californicus* occurred in microhabitats with a high percent cover of western hemlock and lichen, low percent cover of deciduous trees and high total length of decayed logs. *Microtus oregoni* occurred in microhabitats high in percent cover of deciduous herbs, evergreen herbs and deciduous shrubs. Microhabitats where *M. richardsoni* occurred had a high percent of exposed soil, high total length of recently fallen logs and low percent cover of douglas fir. The results of combining the three microtine species in one discriminant procedure indicated that microhabitat separation among the species was significant and was a function of canopy cover of deciduous trees, percent cover of lichen and distance from streamside.

INTRODUCTION

Small mammal distribution and diversity may be influenced by many factors including habitat selection, competition and distribution and abundance of food (*e.g.*, Rosenzweig and Winakur, 1969; Brown, 1973; Dueser and Shugart, 1978). Coexistence of small mammal species may be facilitated by partitioning of food resources, variation in daily and seasonal activity patterns and microhabitat separation (*e.g.*, Brown and Lieberman, 1973; M'Closkey and Fieldwick, 1975; Dueser and Shugart, 1978). Many studies investigating distributional patterns of small mammal species have been conducted with heteromyid rodents in arid environments (Rosenzweig and Winakur, 1969; Brown, 1973; Brown and Lieberman, 1973). These studies suggest that coexistence of heteromyid species is a function of habitat complexity, amount of annual rainfall and ability to partition seed resources. In the desert, seeds provide a year-round resource that can be partitioned along a size gradient. Because seeds are not available year-round in coniferous forests of the Pacific Northwest, we would expect other resources, such as microhabitat, to be important dimensions on which ecologically similar species segregate.

This study examined the microhabitat distribution of *Clethrionomys californicus*, *Microtus oregoni* and *M. richardsoni*, sympatric microtine rodents that are similar in morphology and life history patterns. They are all herbivores. *Clethrionomys californicus* feeds primarily on lichens and subterranean fungi and secondarily on forbs and seeds (Maser *et al.*, 1981). *Microtus oregoni* eats grasses, forbs, huckleberries (*Vaccinium* spp.) and substantial amounts of subterranean fungi (Maser *et al.*, 1981). *Microtus richardsoni* eats forbs and huckleberries. All are primarily nocturnal and subterrestrial (Maser *et al.*, 1981) and are active throughout the year (Johnson and Johnson, 1982). They have similar morphology (Johnson and Johnson, 1982) and a close phylogenetic relationship (Nadler *et al.*, 1978). Discriminant function analyses were used to evaluate significance of microhabitat separation among these species and to determine which habitat variables were important in describing microhabitat differences.

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METHODS

Field research was conducted in the western Cascade Range near Blue River, Oregon, approximately 75 km E of Eugene, Oregon. This area is characterized by well-defined drainages and steep slopes. Annual precipitation ranges from 230–280 cm, 90% of which falls between October and April, and temperatures are moderate with a mean July maximum of 29 C and mean January minimum of -3 C (Franklin and Dyrness, 1971). Soil and bedrock is described in Franklin and Dyrness (1971). Trapping was conducted on four study sites: two along Lookout Creek in the H. J. Andrews Experimental Forest, one along Hagan Creek in the Hagan Research Natural Area, and one along Marten Creek in the Eugene District of the Bureau of Land Management. The Lookout Creek sites were old-growth stands, approximately 250 years old. Hagan and Marten Creek sites were mature forest stands approximately 100 years old.

Douglas fir (*Pseudotsuga menziesii*) was the most abundant conifer on the study sites. Other conifers included western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), silver fir (*Abies amabilis*), grand fir (*A. grandis*) and Pacific yew (*Taxus brevifolia*). The primary deciduous trees were big-leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*) and vine maple (*Acer circinatum*). The predominate ground cover included salal (*Gaultheria shallon*), western swordfern (*Polystichum munitum*), Oregon grape (*Berberis nervosa*) and Oregon oxalis (*Oxalis oregona*). A more detailed description of the habitat can be found in Doyle (1985).

Trapping was conducted from June-November 1982. Sites were trapped on a rotational basis. Four trapping sessions of 9 days each were conducted at each site, for a trap effort of 20,160 trap nights. At each site, two trapping grids were established, one in riparian habitat and one in upland habitat. Each grid consisted of 70 trap stations with 10-m intervals. A Sherman trap (8 x 9 x 23 cm) was placed within 1 m of each grid coordinate and baited with whole oats and sunflower seeds. Scientific and common names of small mammal species follow Jones *et al.* (1982).

Habitat variables were selected on the basis of suspected relevance to microhabitat distribution (Table 1). Trees and logs were analyzed in a 100-m^2 area centered around each trap. Tree measurements included density, canopy cover by species and canopy cover of deciduous vs. evergreen trees. I measured the length and maximum diameter of logs and classified logs according to a five-class decay scale described by Franklin *et al.* (1981).

Herbs and shrubs were analyzed in a 9-m^2 plot centered around each trap. Percent cover was recorded for each vegetative stratum and plant species. Vegetative strata were classified as follows: tree (greater than 5 m), tall shrub (2 m-5 m), small shrub (50 cm-2 m), tall herb (30 cm-50 cm), small herb (less than 30 cm), moss and lichen (less than 5 cm). I measured the number of vegetative strata that exceeded 15% cover, the plant species richness, slope gradient, distance from streamside, and percent of exposed soil, rock, leaf litter, moss and lichen. Deciduous and evergreen components were measured for each vegetative stratum. Herbs were classified in accordance with Mueller-Dombois and Ellenberg (1974) as vegetation less than 50 cm in height; therefore, this category included both deciduous and evergreen components. To determine the quantity of vegetation at varying heights, I used a modified version of the vegetative profile analysis technique described by Nudds (1977). At a constant distance of 5 m, I recorded the proportion of the vegetative profile board obscured by vegetation at varying heights above the ground (Table 1).

Discriminant analysis distinguished between microhabitats that were used by a species and microhabitats that were available but were not used. Discriminant analysis was also used to compare patterns of microhabitat distribution among the three species. For the DFA, presence or absence of a microtine species at a trap station was associated with the corresponding microhabitat variables at that trap station. Total structure coefficients (the correlations between the habitat variables and the discriminant functions) were used to assess the relative contribution of the habitat variables to the discriminant

function (Klecka, 1980). To assess the adequacy of the discriminant function, original observations were classified to determine how many were correctly classified by the variables in the discriminant function (Klecka, 1980). A certain number of observations would be expected to be classified correctly by chance; therefore, the kappa statistic (Titus *et al.*, 1984) was computed to provide the percent of correct predictions beyond the number expected by chance alone. Chi-square tests were used to evaluate differences between microtine use of habitat types and stand ages.

RESULTS

Clethrionomys californicus (285 captures) was the fourth most numerous species captured on the study grids. *Microtus oregoni* (122 captures) and *M. richardsoni* (28 captures) ranked seventh and eighth, respectively, in terms of number of captures. *Tamias townsendii* (739 captures) and *Peromyscus maniculatus* (703 captures) were the most numerous small mammals on the study grids.

Clethrionomys californicus was captured significantly more frequently in upland than riparian habitat (Table 2). Conversely, *Microtus oregoni* was captured significantly more frequently in riparian than upland habitat. *Microtus richardsoni* was caught exclusively in riparian habitat. Both *C. californicus* and *M. richardsoni* were captured significantly more frequently in old-growth stands than in mature forest stands, whereas *M. oregoni* was

TABLE 1.—Designation and description of habitat variables

Variable	Description
STRATNUM	Number of vegetative strata exceeding 15% cover
SPECNUM	Plant species richness
SOILEX	Percent cover of exposed soil
ROCK	Percent cover of exposed rock
LEAFLT	Percent cover of leaf litter
LICHEN	Percent cover of lichen
MOSS	Percent cover of moss
HERBDC	Percent cover of deciduous vegetation < 50 cm in height
HERBEV	Percent cover of evergreen vegetation < 50 cm in height
SHRBDC	Percent cover of deciduous shrubs
SHRBEV	Percent cover of evergreen shrubs
TREEDC	Canopy cover of deciduous trees
TREEEV	Canopy cover of evergreen trees
CREEKDIS	Distance from streamside (m)
ACMACOV	Canopy cover of big-leaf maple, *Acer macrophyllum*
ALRUCOV	Canopy cover of red alder, *Alnus rubra*
PSMECOV	Canopy cover of Douglas-fir, *Pseudotsuga menziesii*
TSHECOV	Canopy cover of western hemlock, *Tsuga heterophylla*
P1	Proportion of vegetation in 0.0-0.25 m layer
P2	Proportion of vegetation in 0.25-0.5 m layer
P3	Proportion of vegetation in 0.05-1.0 m layer
P4	Proportion of vegetation in 1.0-1.5 m layer
P5	Proportion of vegetation in 1.5-2.0 m layer
P6	Proportion of vegetation in 2.0-2.5 m layer
FHD	Based on vegetative profile analysis, foliage height diversity = $1/\Sigma p_i^2$, where P_i is the proportion of vegetation in the ith layer
SNAGNUM	Number of snags in 100 m^2
AVGLOGDI	Average diameter of logs in 100 m^2
NEWLOGS	Total length of recently fallen logs in decomposition classes 1 and 2
OLDLOGS	Total length of decayed logs in decomposition classes 3, 4 and 5
SLOPE	Average of upslope and downslope gradient

captured significantly more often in mature forest stands.

The difference between microhabitats where *Clethrionomys californicus* was caught and those where this species was never caught was highly significant ($P<0.001$) (Table 3). Six variables were selected by stepwise DFA as most effectively distinguishing between microhabitats. Percent cover of lichen, canopy cover of western hemlock and total length of decayed logs (decomposition classes three to five) were the most important positively correlated variables distinguishing between microhabitats used by *C. californicus* and microhabitats available but not used. Canopy cover of deciduous trees was negatively correlated with the discriminant function. Other variables included in the discriminant function were plant species richness and distance from streamside. Using only the six variables in the discriminant function, 70% of the cases were correctly classified as to whether or not *C. californicus* was captured at the trap station (kappa = 32%).

For *Microtus oregoni*, the separation between microhabitat types was also highly significant ($P<0.001$). The three most important variables were the percent cover of evergreen and deciduous herbs and percent cover of deciduous shrubs (Table 3). These variables were positively correlated with the discriminant function. Leaf litter was a less important variable (*i.e.*, less correlated with the discriminant function) and was negatively correlated with the discriminant function. This procedure correctly classified 69% of the observations (kappa = 19%).

For *Microtus richardsoni*, the most important positively correlated variable was the per-

TABLE 2.—Number of captures in riparian vs. upland habitat and in old-growth vs. mature forest stands. Chi-square tests were used to evaluate differences between habitat types $^{*}P<0.01$; $^{**}P<0.001$

Species	Riparian	Upland	Old-growth	Mature
Clethrionomys californicus	82	203**	227	58**
Microtus oregoni	95	27**	44	78*
M. richardsoni	28	0**	25	3**

TABLE 3.—Summary of stepwise discriminant analyses used to distinguish between microhabitats that were used by a species and those that were available but were not used. $^{**}P<0.001$. Mnemonics follow those in Table 1

Variable or characteristic	Total structure coefficients		
	C. californicus	*M. oregoni*	*M. richardsoni*
SPECNUM	0.34		0.36
SOILEX			0.58
LEAFLT		-0.24	
LICHEN	0.58		-0.28
HERBDC		0.69	
HERBEV		0.64	
SHRBDC		0.53	
TREEDC	-0.74		
CREEKDIS	0.25		
PSMECOV			-0.50
TSHECOV	0.73		
NEWLOGS			0.45
OLDLOGS	0.36		
SLOPE			-0.40
Approximate F	21.29**	12.26**	14.40**
Percent correctly classified	70.1	69.2	90.9

cent of exposed soil (Table 3). Highly negatively correlated variables were canopy cover of douglas fir and slope gradient. Additional variables in the discriminant function were plant species richness, percent cover of lichen (negative correlation) and total length of recently fallen logs (decomposition classes one and two). The separation between microhabitat types was highly significant ($P<0.001$) and the procedure classified 91% of the observations correctly (kappa = 29%).

The results of combining the three microtine species in one DFA procedure identified variables effective in distinguishing among the microhabitats used by each species. This procedure produced two highly significant discriminant functions ($P<0.001$) (Table 4). The most important variables on the first discriminant function were percent cover of lichen, canopy cover of deciduous trees and distance from streamside. Additional variables in the first function were percent of exposed soil, deciduous and evergreen herbs and canopy cover of douglas fir. This function accounted for 82% of the discriminating information. Percent cover of evergreen herbs was the most important variable in the second discriminant function. This analysis correctly classified 74% of the observations (kappa = 48%). Estimates of the mean and standard error of the variables included in the discriminant analyses are given in Table 5.

DISCUSSION

Clethrionomys californicus is found in moist coniferous forests dominated by red cedar, western hemlock and douglas fir. The forest canopy in habitats where this vole occurs is often dense (Macnab and Dirks, 1941). This species occurred in both mature and old-growth forest, but was most abundant in old-growth. Captures were more frequent in upland than riparian habitats.

Clethrionomys californicus is generally found in close association with logs. Gashwiler (1959) found that *C. californicus* survived the clearing of trees but only with the presence of numerous cull logs and mounds of wood debris. However, when the logs and debris were burned, the voles disappeared within 1 year. The results of my study indicated that the abundance of *C. californicus* increases with an increased number of highly decayed logs. Protection from predators might be responsible for the association with fallen logs. However, another important factor may be that highly decayed logs contain high concentrations of mycorrhizae (Maser *et al.*, 1978). *Clethrionomys californicus* uses hypogeous fungi of the class Basidiomycetes as a source of food and perhaps water (Ure and Maser, 1982). When fungi become scarce, lichen is used for food. Lichen is also used for nest building (Ure and Maser, 1982). In my study, lichen was significant in the separation of *C. californicus* from non-*C. californicus* microhabitats.

TABLE 4.—Summary of stepwise discriminant analysis used to differentiate among microhabitats used by three vole species. $^{**}P<0.001$. Mnemonics follow those in Table 1

Variable or characteristic	Total structure coefficients	
	Discriminant function 1	Discriminant function 2
SOILEX	-0.43	-0.48
LICHEN	0.52	0.00
HERBDC	-0.49	0.30
HERBEV	-0.18	0.66
TREEDC	-0.68	0.08
CREEKDIS	0.66	-0.12
PSMECOV	0.31	0.43
Approximate F-value	13.48**	–
Percent correctly classified	73.7	–
Percent discriminating information	0.82	0.18

Microtus oregoni occupies habitats associated with moist coniferous forests in montane areas (Hooven, 1971), but it is most abundant in forest edges and brushland habitats and in old fields (Sullivan and Krebs, 1981). Populations are greater in younger successional stages such as clear-cuts than in undisturbed forests (Gashwiler, 1972). Even in forests that are undisturbed by logging and grazing, such as those represented by my study, *M. oregoni* appeared to be more abundant in the younger of the successional stages available. *Microtus oregoni* occurred more frequently in the mature forests in my study areas than in old-growth stands.

Microtus oregoni was captured more frequently in riparian than upland habitats. Association of *M. oregoni* with riparian habitats and early successional stages probably relates to the extensive herbaceous and shrub cover in these habitat types. The percent covers of deciduous herbs, evergreen herbs and deciduous shrubs were the most important variables identifying microhabitats where *M. oregoni* was captured. Selection of microhabitats high in herbaceous cover may be the result of the diet of *M. oregoni*. This species has a flexible diet, but the main component is herbaceous vegetation (Maser *et al.*, 1978). In addition to supplying food, microhabitats with a high percent cover of herbs and shrubs may provide protective cover.

Microtus richardsoni is found along montane streamsides and in marshes, damp meadows and along upland lakes (Anderson *et al.*, 1976). Findley (1951) captured these voles in dry alpine meadows away from water, although they were most numerous along open streams. In my study, *M. richardsoni* was captured exclusively in riparian habitats.

Use of microhabitats adjacent to streams may be due to the associated microclimate of low temperatures and high humidity (Anderson *et al.*, 1976). In addition, water provides food and protection for this semi-aquatic species. Recently fallen logs, which were important in distinguishing microhabitats used by this species, provided additional protective cover. Forbs, a primary component of the diet of this vole, were abundant in the microhabitats adjacent to the stream. High percent of soil exposure in microhabitats used by *Microtus richardsoni* reflected proximity to the stream and incorporation of a portion of the dry stream bed in the habitat analysis.

Dalquest (1948) reported that *Microtus richardsoni* is limited to alpine habitats. Similarly, Hooven (1971) captured this species only in habitats with an open canopy. In my study, *M. richardsoni* was captured in both mature and old-growth forest stands. How-

TABLE 5.—Mean ($\bar{X}$) and standard error (SE) of the habitat variables included in discriminant functions. Sample size equals the number of trap stations that captured a given species. Mnemonics follow those in Table 1

Variable	*C. californicus* (n = 127) $\bar{X}$	SE	*M. oregoni* (n = 41) $\bar{X}$	SE	*M. richardsoni* (n = 11) $\bar{X}$	SE	*Available* (n = 558) $\bar{X}$	SE
SPECNUM	9.6	0.39	8.9	0.70	10.9	1.35	8.8	0.17
SOILEX	2.3	0.67	4.2	1.19	13.0	2.29	4.4	0.37
LEAFLT	16.0	1.86	18.7	3.28	14.4	6.33	19.7	0.97
LICHEN	2.3	0.12	1.4	0.21	0.6	0.40	1.6	0.06
HERBDC	20.3	2.06	41.3	3.62	39.1	7.00	25.3	1.10
HERBEV	16.0	0.01	35.1	3.49	7.7	6.72	17.8	0.94
SHRBDC	36.3	3.07	53.7	5.40	48.6	10.42	38.8	1.47
TREEDC	11.4	2.49	45.6	4.38	72.0	8.46	31.0	1.51
CREEKDIS	108.0	6.32	37.7	11.12	3.8	21.47	88.6	3.65
PSMECOV	37.1	3.06	42.0	5.38	0.0	10.39	38.3	1.56
TSHECOV	39.7	3.10	10.7	5.46	10.5	10.53	22.3	1.36
NEWLOGS	8.0	1.31	8.9	5.29	11.7	4.44	8.2	0.65
OLDLOGS	28.6	1.75	20.5	3.07	13.6	5.94	23.9	0.84
SLOPE	39.6	2.03	33.3	3.57	16.1	6.89	40.5	1.26

ever, within these stands the microhabitats in which this vole occurred were characterized by reduced canopy cover of douglas fir, indicating greater abundance in areas with a more open forest canopy.

Complexity of structure has been said to be important in microhabitat selection by desert rodents (Rosenzweig and Winakur, 1969) and rodents of deciduous forests (Dueser and Shugart, 1978). One measure of habitat complexity, specifically related to the vertical component, is foliage height diversity. Birds and lizards specialize along the vertical component where the environment is vertically complex (MacArthur, 1958; Rand, 1964). Several studies of rodent communities have also suggested that vertical complexity is a significant factor in microhabitat separation (*e.g.*, Rosenzweig and Winakur, 1969; M'Closkey and Fieldwick, 1975). In my study, the mean foliage height diversity in habitats where a given species occurred was similar among the vole species and was not significant in microhabitat separation. Considering the activity patterns of these species (all three species are primarily subterrestrial), it is unlikely that they segregate along the vertical component to any great extent. Except for *Phenacomys*, and to a lesser extent, *Microtus longicaudus*, microtine rodents are not arboreal and therefore would use vertical structure only indirectly.

For both *Clethrionomys californicus* and *Microtus richardsoni*, plant species richness was important in separating microhabitats used from those available. However, this variable was not important in distinguishing among microhabitats selected by the three vole species. This supports the assessment by Rosenzweig and Winakur (1969) that this variable may not be an important component of a successful habitat complexity model.

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