INTRODUCTION

Although riparian habitat occupies only a small proportion of the total land base, it is an important and productive habitat for terrestrial vertebrates (Bull, 1978). The vegetation in this habitat is influenced by streams and associated high water tables and consequently consists of moisture-tolerant or moisture-dependent plants. Streams also influence the microclimate; relative humidity may be higher and temperatures lower with less temperature fluctuation than in surrounding areas. Riparian areas are important in the production of timber, grazing lands, outdoor recreation, mineral resources, and water, creating a high potential for conflict between these resources and wildlife resources (Thomas, 1979).

Relatively little is known about use of riparian habitats by terrestrial vertebrates in montane areas. Riparian research has focused on arid regions of the U.S. and, to some extent, on floodplains of low gradient streams and rivers (Johnson and Jones, 1977; Sands, 1977). It is difficult to extrapolate the results of these studies to areas of the Pacific Northwest because high precipitation results in riparian habitat that is much less distinct from the surrounding habitat. Riparian-related research in montane areas of the Pacific Northwest has focused on influences of streamside vegetation on the aquatic ecosystem with and biomass in riparian habitat. Mean adult weight of *Mustela erminea* was higher in riparian habitat.

Ten of the 12 species for which reproductively active males were detected had a higher percent of adult males in breeding condition in the riparian habitat. Ten of the 13 species for which reproductively active females were detected had a higher percent of adult females in breeding condition in the riparian habitat. Of the 15 species for which juveniles were captured, seven had a higher percent of juveniles in upland habitat, six species had a higher percent in riparian, and two species had an equivalent percent in both habitat types.

CHAPTER I

SMALL MAMMAL USE OF RIPARIAN VS. UPLAND HABITATS

ABSTRACT

This study examined the use of riparian vs. upland habitats by small mammals. Mark-recapture was conducted from 1981 to 1983 in riparian and nearby upland habitats in the western Cascade Range of Oregon. There were 19 small mammal species trapped during the study. Total number of individuals and species richness were both greater in riparian habitat than in upland habitat. Due to the occurrence of several rare species in riparian habitat, species evenness was greater in upland habitat. With the exception of *Scapanus orarius*, all species in the order Insectivora were represented by a higher number of captures and density in riparian habitat. All insectivores had higher mean adult weights and biomass per ha in riparian habitat. Four rodents (*Tamias townsendii*, *Clethrionomys californicus*, *Glaucomys sabrinus*, and *Spermoplilus beecheyi*) had higher numbers of captures, densities, and biomass per ha in upland habitat. Five additional rodents (*Tamiasciurus douglasii*, *Peromyscus maniculatus*, *Microtus oregoni*, *Microtus richardsoni*, and *Zapus trinotatus*) had higher values for these parameters in riparian habitat. All but one member of the order Rodentia had higher mean adult weights in riparian habitat. Two mustelids, *Mustela erminea* and *Mustela frenata*, had higher numbers of captures, densities,

individual were used to assess the role of competition between the species.

Specifically, this study addressed the following questions: (1) Are small mammal diversities, densities, and biomass greater in riparian than in upland habitats? (2) Is a greater proportion of the adult population breeding in riparian than in upland habitats? (3) Is survivorship, or length of residence, greater in riparian than in upland habitats? (4) What are the patterns of microhabitat selection by small mammal species? (5) Are there structural differences among the microhabitats of three locally sympatric microtines and, if so, what environmental variables describe these differences? (6) How do patterns of microtine microhabitat selection relate to the availability of microhabitats? and (7) Does removal of the most abundant small mammal species, *Peromyscus maniculatus*, result in increased abundance, activity levels, or number of stations used per individual in the remaining small mammal species?

gradient floodplains and arid regions, few comprehensive studies of riparian small mammal communities have been conducted.

The first paper of this thesis explores small mammal use of riparian vs. upland habitats in terms of species richness, species diversity, abundance, mean adult weight, survivorship, reproductive activity, and the percent of juveniles in the population. The second paper investigates if microhabitat separation occurs between three sympatric microtine species: *Microtus oregoni*, *M. richardsoni*, and *Clethrionomys californicus*. These species were selected for the study because they are potential competitors due to similarities in morphology and life history patterns. Discriminant analysis was used to evaluate the significance of microhabitat separation and to determine which environmental variables were important in describing microhabitat differences.

The third paper investigates patterns of competition between *Peromyscus maniculatus*, the most abundant species, and the remaining small mammal species. During the 1983 field season, *P. maniculatus* were removed from four of the eight live-trap grids. Previous trapping sessions on the four experimental grids provided temporal controls. Each experimental grid also had a paired control similar in habitat, stand age, and trap effort. Changes in relative abundance, activity levels, and number of trap stations used per

SMALL MAMMAL MICRO- AND MACROHABITAT SELECTION IN STREAMSIDE ECOSYSTEMS

INTRODUCTION

During the summer and fall seasons of 1981 and 1983, mark-recapture was conducted in riparian and upland habitats within old-growth and mature forest stands in the western Cascade Range of Oregon. The purpose of the study was to investigate patterns of small mammal community structure in streamside ecosystems. There were two principal objectives. The first was to understand the significance of riparian habitat in contributing to the stability of small mammal populations in coniferous forests and to determine what environmental factors are responsible for this significance. The second objective was to investigate the role of competition between small mammal species as a process underlying the patterns of small mammal distribution.

Riparian habitat is believed to be one of the most critical habitats for terrestrial wildlife, however, relatively little is known about use of this habitat in montane areas. Research has focused on arid regions and on floodplains of low gradient streams and rivers. Riparian-related research of montane areas in the Pacific Northwest has centered on the aquatic ecosystem with emphasis on fish habitat. Even in low

Chapter III

Chapter II

LIST OF TABLES

Page

Chapter I

Chapter II

LIST OF FIGURES

Page

Chapter I

TABLE OF CONTENTS

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SMALL MAMMAL MICRO- AND MACROHABITAT SELECTION IN STREAMSIDE ECOSYSTEMS

by

Arlene T. Doyle

A THESIS

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"switched" to *T. townsendii* thereby effectively depressing densities of *T. townsendii* on the removal grids.

richardsoni, and *Clethrionomys californicus*, were studied relative to microhabitat separation because they are potential competitors due to similarities in morphology and life history. Discriminant analysis identified significant separation based on cover of lichen and deciduous trees and distance from the creek. Specifically, *C. californicus* selected microhabitats with a high percent cover of lichen and western hemlock and low percent cover of deciduous trees. *M. oregoni* selected microhabitats high in deciduous and evergreen herbs and deciduous shrubs. Microhabitats selected by *M. richardsoni* had a high soil exposure, greater length of recently fallen logs, and reduced cover of Douglas-fir.

To investigate patterns of competition, *Peromyscus maniculatus*, the most abundant small mammal, was removed from four grids in 1983. All species of the order Insectivora increased with the removal of *P. maniculatus* relative to most parameters measured. Captures were significantly higher on removal grids for *Sorex monticolus*, *Sorex bendirii*, *Sorex trowbridgii*, and *Scapanus orarius*. Two rodents, *Zapus trinotatus* and *Glaucomys sabrinus*, also increased with the removal of *P. maniculatus*, suggesting responses to release from exploitative competition. *Tamias townsendii* had significantly fewer captures and individuals on experimental grids. Removal of *P. maniculatus* left *T. townsendii* the most abundant small mammal on experimental grids. It is possible that predators

AN ABSTRACT OF THE THESIS OF

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During summer and fall of 1981 to 1983, mark-recapture was conducted in riparian and upland habitats within old-growth and mature forests in the Cascade Range of Oregon. Number of individuals and species richness were greater in riparian than upland habitat. For most species, the mean adult weights and the percentages of reproductively active males and females were greater in riparian habitat. Insectivora had higher numbers of captures, densities, and biomass per ha in riparian habitat. Four rodents had higher numbers of captures, densities and biomass per ha in upland habitat. An additional five rodents had higher values for these parameters in riparian habitat. Both mustelids captured had higher numbers of captures, densities, and biomass in riparian habitat.

Three sympatric voles, *Microtus oregoni*, *Microtus*

particular emphasis on fish habitat (Meehan et al., 1977; Swanson and Lienkaemper, 1978; Swanson et al., 1976). Even in low gradient floodplains and arid regions, most research has focused on the avian community (Austin, 1970; Caruthers et al., 1974; Dickson, 1978; Gaines, 1974; Hehnke and Stone, 1979; Stamp, 1978; Stauffer and Best, 1980; Stevens et al., 1977). Few comprehensive studies of riparian small mammal communities have been conducted (Boeer and Schmidly, 1977).

The purpose of this study was to define the patterns of small mammal community structure in streamside ecosystems. Specifically, this study addressed the following questions: (1) Are small mammal diversities, densities, and biomass greater in riparian than in upland habitats? (2) Is a greater proportion of the adult population breeding in riparian than in upland habitats? (3) Is survivorship, or length of residence, greater in riparian than in upland habitats? and (4) What are the patterns of microhabitat selection by small mammal species?

Parameters of survivorship and reproduction were investigated because density alone may be misleading in terms of assessing habitat quality (Van Horne, 1983). Habitat quality should be assessed on the basis of success of survival and reproduction. Unless these parameters are investigated, information may not be sufficient to distinguish "source" habitats (habitats responsible for much of the production of juveniles) and "dispersal sinks" (refuge areas where surplus indivudals can disperse to) (Lidicker, 1975; Van Horne, 1983).

Patterns of habitat distribution do not necessarily follow directly from habitat choice. Preferred habitat of a species (e.g., as assessed by laboratory preference tests) may not be available within species dispersal capabilities. In addition, inter- or intraspecific competition may force species into suboptimal habitats. Patterns of predation and the effects of inclement weather can also influence species distributions. Field studies and lab preference tests are required to ascertain habitat choice. Studying habitat preference by *Peromyscus maniculatus*, Wecker (1963) used the rate of travel as an index of the intensity of exploration. Through a series of experiments in enclosures, Wecker determined that early experience reinforced innate habitat preferences in *P. maniculatus*. Rosenzweig (1973) conducted a habitat tailoring experiment to investigate the relationship between habitat structure and the distribution of two species of heteromyid rodents. Holbrook (1979) investigated both habitat preference and interspecific competition by habitat tailoring and small mammal species removals, respectively. Other studies exploring the patterns of competition underlying habitat distribution include those by Abramsky et al. (1979), Abramsky and Sellah (1982), Blaustein (1980), Brown (1971), Chappell (1978), Price (1978), Redfield et al. (1977), and Schroder and Rosenzweig (1975). Lab studies such as those by Getz (1972), have used artificial structures to elucidate the cues utilized in selection of habitats.

METHODS

Study area

Field research was conducted in the western Cascade Range in the vicinity of Blue River, Oregon, approximately 75 km east of Eugene. This area is characterized by well-defined drainages and steep slopes. Soil is primarily a clay loam, volcanic in origin (Gashwiler, 1972). Bedrock is comprised of the Oligocene-Miocene Western Cascade Group (Franklin and Dyrness, 1971).

Annual precipitation ranges from 2,300 mm to 2,800 mm, 90% of which falls between October and April (Franklin and Dyrness, 1971). Above 900 m, snowpacks accumulate to 1 m or more. Temperatures are moderate with a mean July maximum of $29^{o}C$ and mean January minimum of $-3^{o}C$. A more complete description of the soils, climate, and bedrock can be found in Franklin and Dyrness (1971).

Four study sites were selected: two along Lookout Creek, a fourth order (Strahler, 1957) stream on the H. J. Andrews Experimental Forest; one along Hagan Creek, a fourth order stream in the Hagan Research Natural Area; and one along Marten Creek, a fifth order stream in the Eugene District of the Bureau of Land Management. The Upper and Lower Lookout sites are old-growth stands, approximately 250 years old. Hagan and Marten are mature forest stands, approximately 100 years old. Study sites were separated from one another by a distance of at least 2.8 km.

The percent cover of deciduous herbs, shrubs, and trees and of evergreen herbs was significantly greater ($P<0.01$) in riparian than in upland habitat (Table 1). Conversely the percent cover of evergreen shrubs and trees was significantly greater ($P<0.001$) in upland habitat. Upland habitat had a significantly higher ($P<0.001$) percent ground cover of moss. Because riparian habitat included a portion of the streambed, the percent of exposed rock was significantly higher ($P<0.001$) in riparian habitat than in upland habitat.

On the riparian grids, the most frequently occurring herbaceous species were *Oxalis oregana* (Oregon oxalis), *Polystichum munitum* (western sword fern), and *Smilacina stellata* (starry solomon plume)(Table 2). Predominant riparian shrub species were *Rubus ursinus* (trailing blackberry), *Vaccinium parvifolium* (red huckleberry), and *Corylus cornuta* (California hazel). Deciduous tree species, including *Acer macrophyllum* (big-leaf maple), *Acer circinatum* (vine maple), and *Alnus rubra* (red alder), were more abundant in riparian than in upland habitat (Table 3). The most abundant conifers in riparian habitat were *Pseudotsuga menziesii* (Douglas-fir) and *Tsuga heterophylla* (western hemlock).

On the upland grids, *Linnaea borealis* (twin flower) was the most frequent herbaceous species, followed by *Pteridium aquilinum* (bracken fern) and *Smilacina stellata*. The predominant upland shrubs were *Gaultheria shallon* (salal), *Rhododendron macrophyllum* (Pacific rhododendron), *Rubus ursinus*, and *Berberis nervosa* (Oregon grape). *Pseudotsuga menziesii* and *Tsuga heterophylla* were the most frequently occurring upland tree species. Measures of vegetative diversity were greater for riparian than upland grids with respect to foliage height diversity, plant species diversity, richness, and evenness (Table 4).

On the Upper Lookout site, thermographs recorded metereological data on the riparian and upland grids. Neither mean minimum air temperature nor mean night air temperature were markedly different between riparian and upland habitat (Bierlmaier, in litt.). However, both the mean maximum air temperature (Fig. 1) and the absolute range of air temperature (Fig. 2) were consistently higher in upland than in riparian habitat (Bierlmaier, in litt.).

Trapping procedure

Trapping was conducted during the months of July through November of 1981 and June through November of 1982 and 1983. This time period represented a trap effort of 40,152 trap nights. At each of the four sites, two trapping grids were established, one in riparian habitat and one in nearby upland habitat. Riparian and upland grids at a given site were separated from one another by approximately 150 m, depending on the width of the transition zone. Fourth and fifth order streams (Strahler, 1957) were selected because of their influence on the surrounding forest vegetation (Campbell, 1979). The upslope edge of the riparian habitat was identified by a change in plant species composition or relative abundance; the downslope boundary was the water's edge at low flow. The riparian grid was established randomly within the constraint that the grid was oriented perpendicular to the stream to maximize the stream/grid interface.

Due to the relatively high precipitation in western Oregon, there is a large transition zone between the riparian and upland habitat. With increasing distance from the stream, the vegetation of the transition zone becomes increasingly xeric and contains greater quantities of *Berberis nervosa*, *Gaultheria shallon*, and *Pteridium aquilinum*. The upland grids were placed upslope from the riparian grids beyond the transition zone. These grids were established fully within upland habitat as defined by the more xeric, predominantly coniferous community.

In 1981, each grid consisted of 56 trap stations. During 1982 and 1983 each grid was expanded to 70 trap stations. All grids had a grid interval of 10 m. Because of the linearity of the riparian habitat, the Upper Lookout riparian grid was 2 x 35 stations. All other grids were 7 x 10. One large Sherman live trap (8 x 9 x 23 cm) was placed at each trap station within 1 m of the grid coordinate and was baited with a mixture of whole oats and sunflower seeds. Unbaited, unset traps were positioned at the trap stations for at least one week prior to trapping to minimize a neophobic reaction to the traps. Traps were set lightly to effectively sample juveniles as well as adults.

Traps were checked each morning as soon as light was sufficient to process the mammals. Species, sex, age class, weight, and reproductive condition were noted. Males were classified as being reproductively active if their testes were descended into the scrotal sac; females were classified as being reproductively active if their nipples were enlarged. Age classes were determined by body weights. For each species, the minimum weight at which individuals were reproductively active was determined (Table 8). Animals equal to or over this weight were classified as adults. For species for which there were fewer than 15 captures of reproductively active individuals of a given sex, I used the minimum cutpoints reported by Maser et al. (1981) and Burt and Grossenheider (1976) to classify animals as juveniles vs. adults. Each animal was marked by toe clipping prior to release at capture sites. All scientific and common names follow Jones et al. (1982).

Habitat variables

The habitat around each of the 560 trap stations was characterized. Criteria for selecting habitat variables and corresponding measurements were 1) potential relevance to microhabitat distribution, 2) ability to be quickly and accurately measured with minimal disturbance, and 3) repeatability.

There were two levels of habitat analysis around each trap station. Trees, logs, and snags were characterized in a 100-m^2 area centered around each trap. Tree measurements included density, height, diameter at breast height (DBH), and canopy cover by species, as well as canopy cover of all trees. Logs were measured for length and maximum diameter then classified according to a five-class decay scale described by Franklin et al. (1981). Snags were measured for height and DBH then classified on a five-class decay scale based on the texture of exposed wood and the presence of bark, twigs, and large branches.

Centered within each 100-m^2 plot was a 9-m^2 plot within which herbs and shrubs were characterized. The method of vegetative analysis was modified from the releve analysis described by Mueller-Dombois and Ellenberg (1974). Percent cover was recorded for each vegetative stratum. Plant species were listed and grouped with respect to stratum. Each species received a rating according to six cover classes: less than 5, 5 to less than 25, 25 to less than 50, 50 to less than 75, 75 to less than 95, and 95 to 100% (Daubenmire, 1968). Class midpoint values were used in calculations. Also measured were the number of vegetative strata that exceeded 15% cover, the plant species richness, the percent of exposed soil and rock, leaf litter, moss, and lichen, the slope gradient, and the distance to the creek. Deciduous and evergreen components were measured for each vegetative stratum.

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. The quantity of vegetation per layer was converted to the proportion within each layer. Foliage height diversity was then calculated as $1/\Sigma p_i^2$ (where p_i is the proportion of vegetation in the i^{th} layer) to reflect the relative contribution of vegetation at varying heights to the total quantity of vegetation.

The subset of habitat variables used in the analyses are listed in Table 5. Several additional variables were measured but were excluded from the analyses because of high intercorrelations ($\underline{r} \geq 0.70$) with other habitat variables. Combinations of variables, such as ratios, that incorporated the same original data were avoided.

Data analysis

Several variables were used to characterize small mammal communities. These were species richness, species diversity, species evenness, and the total number of individuals. Species diversity and evenness of the small mammal fauna were calculated for each sampling period on each grid. Diversity was calculated using the Shannon-Wiener information index (H') as follows:

$$H' = -\sum_{i=1}^{k} p_i \log_e p_i,$$

where p_i is the proportion of the i^{th} species in the sample (Krebs, 1978). The conditional maximum value of H' (i.e., the value of H' if all species are equal in abundance) is:

$$H' \max = \log_e S,$$

where S equals the number of species in the sample. Pielou's index (J') was used as a measure of evenness and was calculated as follows:

$$J' = \frac{H'}{H' \max} .$$

Statistical comparisons of means of diversity and evenness between habitats were performed with a t test.

Species composition was assessed using frequency of captures and analyzed in relation to habitat types using chi-square tests. Density was calculated for each species on each grid for each sampling period by dividing the total number of individuals captured by an area equal to the area of the grid with a border one-half the width of the grid interval. Density estimates (number of individuals per ha) were converted to biomass density (g live wt/ha) by multiplying density by the mean weight for each species for the specific habitat type. Mean adult weight was used as an indicator of habitat quality (Van Horne, 1982). Significant differences between riparian and upland habitat for these variables were assessed using t tests.

The length of breeding season was defined as the time between the earliest date of capture of a reproductively active individual and the date of the last capture of a reproductively active individual.

The mean length of time between the first and final captures of individuals was used as an index of the minimum survival time, or length of residence, in a study site. Whether an individual died or left the study site could not be distinguished in this study. To minimize inclusion of transient individuals, the values exclude individuals that were captured only once during the three-year period.

Spearman's rank correlation coefficients (Sokal and Rohlf, 1981) were used to assess significant correlations ($\underline{P}<0.01$) between the number of captures per 100 trap nights at each trap station and the corresponding habitat variables (for species for which there was sufficient data).

For habitat variables, t tests were used to document significant differences between riparian and upland habitat for the percent cover of ground cover, vegetative strata, and tree species.

RESULTS AND DISCUSSION

Order Insectivora

The most frequently captured insectivores were *Sorex trowbridgii*, *Sorex monticolus*, *Neurotrichus gibbsii*, and *Scapanus orarius*. *Sorex trowbridgii*, Trowbridge's shrew, was the most prevalent shrew; 331 individuals were captured representing 14.3% of all individuals of small mammal species captured. *S. trowbridgii* is found primarily in the coniferous forests of the Pacific coast (Junge and Hoffmann, 1981). Previous studies have shown that although this shrew is frequently found far from water, it is most numerous in moist areas (Dalquest, 1941; Ingles, 1965). Results of the present study agree with these findings. *S. trowbridgii* was captured 1.3 times more frequently in riparian than in upland habitat ($P<0.05$) (Fig. 3). This species was represented by more individuals per ha in riparian habitat, although this difference was not statistically significant (Table 6). The values of several other parameters also suggested that *S. trowbridgii* is predominantly a riparian species. Mean adult weight was higher in riparian habitat (Table 8) as was mean biomass per ha (Table 9), and minimum survival time (Table 10). Percent of adult males in breeding condition was higher in riparian (Fig. 4), although this value was higher in upland for adult females (Fig. 5). The duration of the breeding season was longer in riparian habitat for males (Table 11), but, again, the reverse was true for females (Table 12). The percent of juveniles was higher in upland habitat (Table 13).

Some of the factors reported as influencing the local distribution of these shrews are litter, ground cover, and shrubby vegetation (Gashwiler, 1970; Hooven and Black, 1976; Jameson, 1955). Maguire (1982) reported that mesic areas with closed canopies and rich in duff and decayed wood were the primary microhabitats of this species. The present study supports the association of *S. trowbridgii* with shrubby vegetation, specifically evergreen shrubs. The abundance of *S. trowbridgii* was also significantly correlated with a high canopy cover of deciduous trees and low percent cover of lichen.

Sorex monticolus, the dusky or montane shrew, was represented by 226 individuals (9.8% of the total). This species is found primarily in the mountains of western North America (Junge and Hoffman, 1981) in moisture gradients ranging from dry hillslopes to rain forests (Burt and Grossenheider, 1976). Despite this range in moisture gradients, *S. monticolus* was captured 2.4 times more frequently in riparian than in upland habitat ($P<0.001$) (Fig. 3). Both the number of individuals per ha and the biomass per ha were significantly higher ($P<0.01$) in riparian habitat (Tables 7 and 9). This is consistent with Ingles (1965) and Whitaker (1980) who reported that *S. monticolus* is most numerous in the moist vegetation surrounding streams. The mean adult weight was also higher in riparian habitat (Table 8).

Minimum survival time was greatest in upland habitat (Table 10). As with *S. trowbridgii*, the percent of adult males in breeding condition was higher in riparian (Fig. 4) while the percent of adult females in breeding condition was higher in upland (Fig. 5). Both males (Table 11) and females (Table 12) had a longer mean duration of breeding season in riparian habitat. Values for percent of juveniles (Table 13) and the percent of females in breeding condition were highest in upland habitat (Fig. 5).

Ingles (1965) reported that *S. monticolus* occupied microhabitats that were overgrown thickly with willows and tall sedges. Although these plant species were not present in substantial quantities on my study areas, the study does support the association of *S. monticolus* with thick vegetative cover. The abundance of *S. monticolus* was significantly correlated with a high percent cover of deciduous and evergreen herbs, deciduous shrubs, and deciduous trees (Table 14). *S. monticolus* was significantly negatively correlated with evergreen shrubs and trees, distance to the creek, and percent cover of lichen.

Neurotrichus gibbsii, the shrew-mole, was the most abundant mole species. Forty-one individuals (1.8% of the total) were captured. *N. gibbsii* is found in coniferous forests of the Pacific Northwest (Whitaker, 1980). Although it occurs in dry coniferous forests, it is most numerous in mesic habitats

(Dalquest, 1941). This species was captured 1.6 times more frequently in riparian habitatthan in upland habitat (Fig. 2). N. gibbsii was represented by a higher number of individuals per ha (Table 6) and higher biomass per ha (Table 9) in riparian habitat.

Only one of the 41 individuals was captured more than once. This individual was in the upland habitat and was captured twice over a 12-day interval (Table 10). The percent of adult females in breeding condition was higher in riparian habitat (Fig. 5); for adult males this value was equivalent for the two habitat types (Fig. 4). Detection of adults in breeding condition was infrequent; duration of the breeding season was not markedly longer in riparian than in upland habitat for either sex (Tables 11 and 12). The proportion of juveniles in the population was greater in riparian habitat (Table 13).

Neurotrichus gibbsii is a shallow burrower in soils rich in organic matter (Ingles, 1965) and is also active on the surface of the ground (Whitaker et al., 1979). Although Whitaker et al. (1979) reported that N. gibbsii is associated with large, highly decayed logs, correlations were not significant with either the total length of highly decayed logs or with average log diameter. The abundance of N. gibbsii was significantly negatively correlated with percent cover of lichen and number of snags (Table 14).

The total catch of Scapanus orarius, the coast mole, was 21 individuals, slightly less than one percent of all animals caught.

S. orarius occurs in a wide variety of habitats including meadows and deciduous and coniferous forests of the Pacific Northwest (Ingles, 1965; Maser et al., 1981; Whitaker, 1980). This study supported the adaptation to divergent habitat types. This species was captured almost equally in riparian and upland habitats (48.5% in riparian and 51.5% in upland) (Fig. 3). Mean number of individuals per ha was also nearly equivalent between the two habitat types (Table 6). Mean adult weight was higher in riparian habitat (Table 8) as was mean biomass per ha (Table 9). Conversely, minimum survival time was greater in upland habitat (Table 10). No adult females were captured in breeding condition in either habitat type and no adult males were captured in breeding condition in riparian habitat (Fig. 4). However, in upland habitat, adult males were in breeding condition in 20.0% of the captures. No juveniles were captured in riparian habitat; juveniles represented 17.6% of the captures in upland habitats (Table 13). The abundance of S. orarius was most highly correlated ($P<0.05$) with a low percent cover of evergreen trees and lichen and a high percent cover of exposed soil (Table 14).

Sorex vagrans, the vagrant shrew, was caught sporadically. Only three individuals were captured, representing 0.13% of the total catch. S. vagrans occurs in forested regions of western North America primarily in mesic habitats including marshes, forests, bogs, wet meadows, and along forest streams (Burt and Grossenheider, 1976; Junge and Hoffmann, 1981). Dalquest (1941) reported that of several hundred captures, he captured only two of these shrews in dry woods and these two were in woods close to water. The captures of this species in the present study occurred within 4.6 m of the stream (mean distance was 3.1 m). These individuals were adults, none of which was in breeding condition. The non-breeding condition and the low number of captures suggest that the habitats represented in the study sites only poorly met the habitat requirements of this species, which are apparently best met in heavily grassed meadowlike situations (Clothier, 1955; Hooven et al., 1975) or in thick vegetation of *Salix*-*Scirpus* habitat (Ingles, 1965).

Sorex palustris, the water shrew, was represented by two individuals (0.09% of the total catch). *S. palustris* is a montane shrew found throughout northern U.S. and much of Canada (Burt and Grossenheider, 1976; Conaway, 1952). It is the most aquatic member of its genus and is closely restricted to the vicinity of streams and ponds (Junge and Hoffmann, 1981) particularly under the cover of overhanging banks and log debris (Conaway, 1952). In this study, both captures were within 3.0 m of the creek (mean distance was 2.0 m). Both individuals were adults; neither was in breeding condition.

Sorex bendirii, the Pacific water or marsh shrew, was also represented by two individuals, an adult male and adult female both in breeding condition. These individuals were captured together in riparian habitat at 24.6 m from the creek in a site with a high percent cover of humus.

Order Rodentia

The most frequently captured species of the order Rodentia were *Peromyscus maniculatus*, *Tamias townsendii*, *Zapus trinotatus*, and *Clethrionomys californicus*. *P. maniculatus*, the deer mouse, was the most numerous species relative to both the number of individuals and the number of captures. With a total of 771 individuals captured, *P. maniculatus* represented 33.3% of the total number of animals caught. *P. maniculatus* is a ubiquitous species found in nearly all habitats and life zones (Ingles, 1965; Maser et al., 1981). Despite the ubiquity of this species, Bailey (1936) reports open timber and brush-land as its primary habitats. Maguire (1982) reports this species as being more abundant in mesic areas of open canopies and high herbaceous cover. In my study, *P. maniculatus* was represented by significantly more captures ($P<0.001$) (Fig. 6) and more individuals per ha ($P<0.01$) in riparian habitat (Table 6), an area with significantly higher cover of both deciduous and evergreen herbs (Table 1).

In addition to being more numerous in riparian habitat, *P. maniculatus* had higher values in riparian habitat for almost all parameters measured. Mean adult weight was significantly higher in riparian ($P<0.001$) (Table 8). Mean biomass per ha was nearly twice as great in riparian habitat ($P<0.01$) (Table 9); minimum survival time was also greater in riparian habitat (Table 10).

Percent of adult males (Fig. 7) and females (Fig. 8) in breeding condition was significantly higher ($\underline{P}<0.001$) in riparian than upland habitat. Although mean duration of the breeding season was longer in riparian for females (Table 12), this period was longer in upland for males (Table 11). Significantly more juveniles ($\underline{P}<0.001$) were caught in upland habitat (Table 13).

Goodwin and Hungerford (1979) found a high correlation between density of P. maniculatus and cover of logs and stumps. In this study, abundance was significantly correlated with average log diameter and with the total length of decayed logs in decomposition classes three through five (Table 14). P. maniculatus was also significantly positively correlated with plant species richness, and with percent cover of rock, lichen, and deciduous herbs and shrubs. Abundance was significantly negatively correlated with slope gradient, distance to the creek, and percent cover of leaf litter, evergreen shrubs, and evergreen trees.

A total of 343 individuals of Tamias townsendii, Townsend's chipmunk, was captured (14.8% of all small mammals captured). This species occurs in dense hardwood forests and humid coniferous forests of the Pacific coast (Gashwiler, 1976; Whitaker, 1980) and is the only western chipmunk that is able to live deep within undisturbed forest (Tevis, 1956). T. townsendii was captured more frequently in upland habitat ($\underline{P}<0.05$)(Fig. 6). Mean number individuals per ha (Table 6) and biomass per ha (Table 9) was greater (although not significantly) in upland habitat (Table 6). Conversely, mean adult weight was significantly higher ($\underline{P}<0.05$) in riparian habitat (Table 8).

Minimum survival time was virtually equivalent between habitat types (90.3 days in riparian as compared to 90.2 days in upland)(Table 10). Percent of adult males (Fig. 7) and adult females (Fig. 8) in breeding condition was significantly higher ($\underline{P}<0.05$) in riparian habitat. Mean length of breeding season was also greater in riparian habitat for both males and females (Tables 11 and 12). Upland habitat contained a greater percent of juveniles (Table 13).

Tevis (1956) reported that *T. townsendii* increases with increasing quantities of herbaceous and shrubby vegetation. In the present study, this chipmunk was highly correlated with evergreen herbs, shrubs, and trees (Table 14). It was also highly correlated to the woody component of the environment, specifically, number of snags, average log diameter, and total length of highly decayed logs. In addition, *T. townsendii* was significantly positively correlated with slope gradient and percent cover of lichen and negatively correlated with number of vegetative strata and percent cover of exposed soil, deciduous herbs, and deciduous trees.

The Pacific jumping mouse, *Zapus trinotatus* was represented by 194 individuals (8.4% of the total). *Z. trinotatus* occurs in marshy areas, open meadows, and forests of the Pacific Northwest

(Burt and Grossenheider, 1976; Ingles, 1965). According to Maser et al. (1981), this species is most abundant in alder/salmonberry, riparian alder, and skunk-cabbage marsh habitats. Hooven (1971) also found *Z. trinotatus* most abundant in mesic habitats; 39 of 54 captures occurred within 9.1 m of water. In my study, *Z. trinotatus* was captured 4.9 times more often in riparian habitat ($P<0.001$). The mean number of individuals per ha (Table 6) and biomass per ha (Table 9) were also significantly greater in riparian habitat ($P<0.01$ and $P<0.001$, respectively).

In addition to being more numerous in riparian habitat, *Z. trinotatus* had higher values in riparian habitat for several other parameters. These included mean adult weight (Table 8), minimum survival time (Table 10), percent of adult males and females in breeding condition (Figs. 7 and 8), and the duration of the breeding season for both males and females (Tables 11 and 12). Conversely, the percent of juveniles in the population was greater in upland habitat (Table 13).

With respect to microhabitat, Ingles (1965) reported that *Z. trinotatus* prefers grassy wet places. The frequency of grass on the study plots was 26.8% in the riparian compared with 5.0% in the upland habitat; however, this specific variable was not significantly correlated with abundance of *Z. trinotatus*. This species was significantly positively correlated with number of vegetative strata, plant species richness, foliage height diversity, and percent cover of deciduous herbs, shrubs, and trees

(Table 14). Abundance was significantly negatively correlated with slope gradient, distance to the creek, and percent cover of moss, evergreen shrubs, and evergreen trees.

Clethrionomys californicus, the western red-backed vole, was represented by 152 individuals (6.6% of the total). *C. californicus* is found in moist coniferous forests of the Pacific coast (Macnab and Dirks, 1941). The results of the present study indicate that this vole is predominantly an upland species. It was captured 3.3 times more often in upland habitat ($P<0.001$) (Fig. 6). Mean number of individuals per ha (Table 6) and biomass per ha (Table 9) were both significantly greater in upland habitat ($P<0.001$).

Conversely, the percent of adult females in breeding condition (Fig. 8) and the mean adult weight (Table 8) were both significantly higher in riparian habitat ($P<0.01$ and $P<0.05$, repectively). Minimum survival time (Table 10), the percent of adult males in breeding condition (Fig. 7), and the percent of juveniles (Table 13) were also greater in riparian habitat (although not significantly). However, the mean duration of the breeding season was greater in the upland for both sexes (Tables 11 and 12).

The abundance of *C. californicus* was significantly positively correlated with number of snags, distance to the creek, and with percent cover of lichen, moss, and evergreen shrubs and trees (Table 14). Abundance was significantly negatively correlated with number of vegetative strata, foliage height diversity, and percent of exposed soil, leaf litter, and deciduous trees.

One hundred and sixteen individuals of M. oregoni, the creeping vole, were captured (5.0% of the total). M. oregoni occupies all habitats associated with moist coniferous forests in montane areas in the Pacific Northwest (Goertz, 1964; Hooven, 1971). It is most abundant in forest edges and brushland habitats (Goertz, 1964). Populations are greater in clearcuts than in undisturbed forests (Gashwiler, 1972). Goertz (1964) reported that M. oregoni seemed to prefer cutover areas followed by woodland, glade, forest, south slope, and riparian, in that order. Whitaker (1980) also reported a preference for dryer upland slopes. By contrast, I found that M. oregoni was predominantly a riparian species. This vole was captured 3.5 times more often in riparian habitat ($P<0.001$) (Fig. 6). The mean number of individuals per ha (Table 6) and biomass per ha (Table 9) were also significantly higher ($P<0.01$ and $P<0.001$, respectively) in riparian habitat.

In addition to being more numerous in riparian habitat, mean adult weight was significantly higher ($P<0.01$) in riparian habitat (Table 8). Minimum survival time was 1.6 times greater in riparian than upland habitat (Table 10). The percent of adult males and females in breeding condition (Figs. 7 and 8) and the duration of the breeding season (Tables 11 and 12) were all higher in riparian habitat. The percent of juveniles in the population was equivalent for both habitat types (Table 13).

The association of _M. oregoni_ with riparian habitat and early successional stages probably relates to the extensive herbaceous and shrub cover in these habitat types (Dyrness, 1965; Gashwiler, 1972). Deciduous and evergreen herbs and deciduous shrubs were highly correlated with the abundance of _M. oregoni_ (Table 14). Selection of microhabitats high in herbaceous cover probably reflects the diet of _M. oregoni_. This species has a flexible diet that includes huckleberries and hypogeous fungi, but the main component of the diet is herbaceous vegetation (Maser et al., 1978). The abundance of _M. oregoni_ was also significantly positively correlated with the number of vegetative strata and percent cover of deciduous trees and negatively correlated with slope gradient, distance to the creek, and percent cover of evergreen shrubs.

Seventeen individuals of _Microtus richardsoni_, the water vole, were captured (0.73% of the total). _M. richardsoni_ is found primarily in montane streamsides (Anderson et al., 1976; Findley, 1951; Murie, 1960; Rassmussen and Chamberlain, 1959; Rust, 1946) as well as in marshes, damp meadows, and along upland lakes in the Northwest (Ingles, 1965; Whitaker, 1980). Findley (1951) found _M. richardsoni_ most numerous along open streams, although he also captured these voles in dry, alpine meadows away from water. In the present study, _M. richardsoni_ was captured on 119 occasions, all of which were in riparian habitat (Fig. 6). Minimum survival time was 80.5 days (Table 10). About 31% of the adult males and 63% of adult females were in breeding condition (Figs. 7 and 8). Approximately 13% of the population were juveniles (Table 13).

Abundance of M. richardsoni was significantly positively correlated with plant species richness, total length of recently fallen logs, and percent cover of exposed rock, deciduous herbs, and deciduous shrubs, and significantly negatively correlated with slope gradient, distance to the creek, and percent cover of leaf litter, evergreen shrubs, and evergreen trees (Table 14).

The mountain streams with which this species is associated produce a microclimate of relatively consistent low temperatures and high humidity. Runways frequently appear to be saturated (Anderson et al., 1976). Thus the water content of the soil and atmosphere may be very important to this species. In addition, M. richardsoni swims readily and may be dependent on water for protection (Bailey, 1936). Newly fallen logs which characterize the microhabitats selected by this species also provide protective cover. Forbs, a primary component of the diet of this vole, are abundant in the microhabitats adjacent to the stream.

Fifty-two individuals of Glaucomys sabrinus, the northern flying squirrel, were captured (2.7% of the total). G. sabrinus is found in coniferous and mixed coniferous/deciduous forests (Dalquest, 1948; Ingles, 1965; Whitaker, 1980). Although not statistically significant, the number of captures (Fig. 6), number of individuals per ha (Table 6), and biomass per ha (Table 9) were all higher in the upland. Minimum survival time was 2.3 times longer in upland habitat (Table 10). The length of the breeding season for females was nearly twice as great in upland habitat (Table 12).

Conversely, mean adult weight was significantly higher ($\underline{P}<0.01$) in riparian habitat (Table 8). The percent of males (Fig. 7) and females (Fig. 8) in breeding condition and the length of the breeding season for males (Table 11) was greater in riparian habitat. The percent of juveniles in the population was also greater in riparian habitat (Table 13). Abundance of G. sabrinus was significantly positively correlated with slope gradient and percent cover of evergreen shrubs and trees and negatively correlated with percent cover of deciduous herbs and trees (Table 14).

Eight individuals of Neotoma cinerea, the bushy-tailed woodrat, were captured (0.35% of the total). This species is found in coniferous forests of western U.S. and Canada (Whitaker, 1980) primarily in sheltered retreats among cliffs or rock talus (Bailey, 1936; Burt and Grossenheider, 1976; Dalquest, 1948; Hooven, 1971; Whitaker, 1980). Where rocky habitats are limited, N. cinerea lives in log debris, hollow trees and logs, and in nests constructed of sticks as much as 15 m up in a tree (Maser, 1966). N. cinerea was captured 15 times, with 53.3% of these captures being in the upland (Fig. 4). There was an equivalent number of individuals per ha in the two habitat types (Table 6).

Mean adult weight (Table 8), biomass per ha (Table 9), and minimum survival time (Table 10) were all greater in riparian habitat. There were only three captures of reproductively active individuals (Tables 11 and 12); none of these individuals was considered adult according to minimum cutpoints reported by Maser et al. (1981). Percent of juveniles was higher in riparian habitat (Table 13). Although none of the correlations were statistically significant at the 0.01 level, the abundance of *N. cinerea* was most highly positively correlated with average log diameter and foliage height diversity ($\underline{P}<0.05$) and negatively correlated with slope gradient and percent cover of exposed rock ($\underline{P}<0.05$).

Tamiasciurus douglasii, Douglas' squirrel, was represented by only four individuals (0.17% of the total). This species is found in moist coniferous forests of the Pacific Northwest (Burt and Grossenheider, 1976; Dalquest, 1948). *T. douglasii* was captured only five times, four times in riparian and once in upland habitat (Fig. 6). Mean number of individuals per ha was greater for riparian habitat (Table 6). All individuals captured were juveniles (Table 13).

Based on visual observations and calls, this species was abundant on the study sites. However, this species is large enough so that it is only sporadically captured (then only as juveniles) in even the large Sherman live traps. As a result, captures of this species were considered only incidental and relative proportions of captures in the two habitat types may not reflect the actual proportions in the habitats.

Only one *Spermophilus beecheyi*, the California ground squirrel, was captured. This capture occurred in upland habitat and was an adult individual that was not in breeding condition. *S. beecheyi* is found primarily in open habitats such as pastures, grainfields, and early seral stages after logging or burning (Burt and Grossenheider, 1976; Hooven, 1971; Maser et al., 1981) and is generally not found in dense, forested areas such as those present in the study area.

Order Carnivora

Twenty-eight *Mustela erminea*, the ermine, were captured (1.2% of the total). *M. erminea* is found in a variety of boreal habitats from agricultural lowlands, woodlands, and meadows to montane habitats (Svendsen, 1982; Ingles, 1965). Maser et al. (1981) found *M. erminea* most abundant in alder/salmonberry and riparian alder habitats. The present study also indicated a higher abundance of *M. erminea* in riparian habitat. *M. erminea* was captured on 31 occasions; most of these captures were in riparian habitat ($P<0.001$) (Fig. 3). This weasel was represented by a significantly higher number of individuals per ha (Table 6) and biomass per ha (Table 9) in riparian habitat ($P<0.05$ and $P<0.01$, respectively).

In addition to being more numerous in riparian habitat, values for several other parameters were also higher in riparian habitat. These include mean adult weight (Table 8), minimum survival time (Table 10), percent of adult females in breeding condition (Fig. 5), and percent of juveniles in the population (Table 13). There were no reproductively active males detected in either habitat. Abundance of *M. erminea* was significantly positively correlated with evergreen herbs and negatively correlated with evergreen shrubs (Table 14).

Only one *Mustela frenata*, the long-tailed weasel, was captured. This species is found in all habitats near water (Burt and Grossenheider, 1976), particularly in the more advanced successional stages (Simms, 1979). *M. frenata* was captured in the riparian habitat at a distance of 2.0 m from the creek. This individual was a juvenile female and was not in breeding condition.

Species diversity

Measures of diversity were calculated and are presented in Table 15. Small mammal species richness was greater in riparian than in upland habitat for 1981 and 1982 and equivalent between the two habitats in 1983. For all three years, the total number of individuals was about 1.5 times as high in riparian as in upland habitat. Conversely, the evenness index, based on Pielou's J, was higher in the upland for all three years, indicating that the number of individuals per species was more evenly distributed in the upland.

The Shannon-Wiener diversity index, based on information theory, is a function of both species richness and evenness (Hurlbert, 1971). The more species and the more nearly even their distribution, the greater this diversity index will be. Maximum diversity is obtained when all species are present in equal numbers (Table 15) (Hair, 1980). The Shannon-Wiener index was used rather than Simpson's index because the latter index is heavily dependent on the most abundant species in the community (Smith and Grassle, 1977). Simpson's index is appropriate when the evenness of distribution of a few abundant species is of primary interest, rather than the overall evenness of distribution of all species. Despite greater sensitivity to changes in the abundance of rare species, the presence of several rare species (e.g., *Sorex bendirii*, *S. palustris* and *Mustela frenata*, which were never captured in the upland habitat) and the high number of *Peromyscus maniculatus* in riparian habitat contributed to the unevenness of species distributions and lowered the value of the diversity index. Diversity was not significantly greater in riparian habitat for either 1982 or 1983, and in 1981 was actually lower in riparian habitat (although this difference was not significant). This illustrates one of the difficulties inherent in utilizing a single measure, e.g., the Shannon-Wiener diversity index, to try to encapsulate habitat quality.

Source *vs*. "sink" habitats

Although the current study did not specifically address the use of source vs. sink habitats, there were several species in this study that warrant investigation into the question of riparian habitat as a source and upland habitat as a dispersal sink. "Dispersal sinks" may develop if social interactions prevent subordinant individuals from entering into, or remaining in, high-quality habitats (Lidicker, 1975; Van Horne, 1983). Sinks are refuge areas that may be marginal, or even unsuitable, habitats where surplus individuals can disperse to and where survivorship and reproduction may be poor relative to high-quality habitats. Movement into these habitats may reflect maximization of individual fitness if high densities or high potential conflict with dominant individuals would reduce individual survivorship and reproduction in high-quality habitats (Fretwell and Lucas, 1969).

Use of dispersal sinks by small mammals was suggested in a study of *Peromyscus maniculatus* in southeastern Alaska (Van Horne, 1982). Van Horne evaluated two different habitats for both adults and juveniles. High-density adult habitat was characterized by high over-winter survival for individual juveniles as well as adults. Conversely, high-density juvenile habitat was characterized by low over-winter survival for both juveniles and adults. In addition, adult male weights were higher on the grid containing mostly high density adult habitat. Dispersal sinks have been suggested for other species including Lemmus lemmus, the lemming (DeKock et al., 1969), Vulpes vulpes, the red fox (Von Schantz, 1981), Tamias amoenus, the yellow-pine chipmunk (States, 1976) and a variety of birds (Atwood, 1980; Carrick, 1963; Fretwell, 1969; Krebs, 1971; O'Connor, 1981).

In the present study, there were at least four rodent species for which the data indicate that upland habitats may serve as a sink for juveniles dispersing from riparian habitats. These species included Tamias townsendii, Glaucomys sabrinus, Peromyscus maniculatus, and Zapus trinotatus. For each of these species, there was a higher percent of adult males and females in breeding condition in riparian habitat and a higher percent of juveniles in upland habitat. An alternative hypothesis is that juvenile survivorship is higher in the upland habitat.

Two species in the order Insectivora also warrant investigation into the question of riparian habitat as a source and upland habitat as a sink. In these two species, Sorex monticolus and S. trowbridgii, the percent of reproductively active adult males was higher in riparian habitat, whereas the percent of juveniles and of reproductively active adult females was greater in upland habitat. Reproductively active males may be dominant to both juveniles and adult females and thereby secure more optimal habitat.

Summary

With the exception of *Scapanus orarius*, all species in the order Insectivora were represented by a higher number of captures and density in riparian habitat. All insectivores had higher mean adult weights and biomass per ha in riparian habitat. Four rodents (*Tamias townsendii*, *Glaucomys sabrinus*, *Clethrionomys californicus*, and *Spermophilus beecheyi*) had higher numbers of captures, densities, and biomass per ha in upland habitat. Five additional rodents (*Tamiasciurus douglasii*, *Peromyscus maniculatus*, *Microtus oregoni*, *Microtus richardsoni*, and *Zapus trinotatus*) had higher values for these parameters in riparian habitat. All but one member of the order Rodentia had higher mean adult weights in riparian habitat. Two mustelids, *Mustela erminea* and *Mustela frenata*, had higher numbers of captures, densities, and biomass in riparian habitat. Mean adult weight was higher in riparian habitat for *Mustela erminea*.

Ten of the 12 species for which reproductively active males were detected had a higher percent of adult males in breeding condition in the riparian habitat. The remaining species showed an equivalent proportion of breeding adults in both habitat types. Ten of 13 species for which reproductively active females were detected had a higher percent of adult females in breeding condition in the riparian habitat. The data indicate that several species, including *Tamias townsendii*, *Glaucomys sabrinus*, *Peromyscus maniculatus*, and *Zapus trinotatus*, warrant investigation into the question of riparian habitat as a source and upland habitat as a dispersal sink.

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Chapter I

Table 1.--Mean percent cover (and standard error) of vegetative strata and ground cover by habitat. T tests were used to document significant differences between riparian and upland habitat. $*P<0.05$; $**P<0.01$; $***P<0.001$.

Vegetative strata	Mean percent cover		
	Riparian (n=280)	Upland (n=280)	
Herbs			
deciduous	36.62 (1.7)	13.76 (1.1)	***
evergreen	20.86 (1.4)	14.84 (1.2)	**
Shrubs			
deciduous	50.45 (2.1)	26.91 (1.8)	***
evergreen	6.72 (0.9)	44.10 (2.1)	***
Tree (overall)	75.89 (1.7)	81.55 (1.3)	**
deciduous	48.11 (2.4)	13.98 (1.4)	***
evergreen	40.19 (2.0)	77.17 (1.4)	***
Ground cover			
bare soil	5.00 (0.6)	3.84 (0.5)	

Chapter I

Table 1.--(cont., page 2)

Vegetative strata	Mean percent cover Riparian (n=280)	Upland (n=280)	
Ground cover (cont.)			
leaf litter	18.37 (1.4)	21.13 (1.4)	
lichen	1.52 (0.1)	1.75 (0.1)	
log	8.13 (1.0)	7.45 (0.9)	
moss	32.70 (1.7)	47.54 (1.9)	***
rock	7.85 (1.0)	1.75 (0.4)	***

Table 2.--Frequency of forbs and shrubs for most abundant species (occuring at 10 or more stations). Chisquare tests were used to document significant differences between riparian and upland habitat. *$P<0.05$; **$P<0.01$; ***$P<0.001$.

Plant species	Common name	Frequency	
		Riparian (n=280)	Upland (n=280)
Forbs:			
Achlys triphylla	Deerfoot vanillaleaf	15.4	10.0
Adiantum pedatum	Maidenhair-fern	15.4	0.0
Anemone deltoidea	Western white anemone	4.6	10.0
Asarum caudatum	Western wild ginger	17.5	1.4
Athrium filix-femina	Ladyfern	34.3	0.7
Chimaphila spp.	Prince's pine	3.6	23.2
Clintonia uniflora	Queencup beadlily	31.8	22.1
Coptis laciniata	Western goldthread	5.4	8.6
Cornus canadensis	Bunchberry dogwood	17.9	25.0
Galium spp.	Bedstraw	31.1	7.9
Goodyera oblongifolia	Rattlesnake plantain	3.6	10.4
Graminaceae	Grasses	26.8	5.0
Hydrophyllum tenuipes	Waterleaf	17.1	0.0
Linnaea borealis	Twin flower	15.7	37.5
Oxalis oregana	Oregon oxalis	71.1	0.4

Chapter I

Table 2.--(cont., page 2)

Plant species	Common name	Frequency	
		Riparian (n=280)	Upland (n=280)
Polystichum munitum	Sword fern	67.1	19.6
Pteridium aquilinum	Bracken fern	3.2	31.8
Smilacina stellata	Starry solomon plume	44.6	27.1
Tiarella unifoliata	Western coolwort	24.3	13.2
Tolmiea menziesii	Pig-a-back	32.9	1.4
Trillium ovatum	Pacific trillium	11.8	6.8
Vancouveria hexandra	White inside-out-flower	24.3	5.7
Viola sempervirens	Evergreen violet	9.6	18.9
Xerophyllum tenax	Beargrass	0.0	12.9
Shrubs:			
Berberis nervosa	Oregon grape	13.2	38.6
Castanopsis chrysophylla	Golden chinkapin	0.7	15.0
Corylus cornuta	California hazel	28.9	10.7
Gaultheria shallon	Salal	5.0	57.9
Oplopanax horridum	Devil's club	15.0	0.0
Osmaronia cerasiformis	Indian plum	10.7	1.4
Rhododendron macrophyllum	Pacific rhododendron	0.7	45.4
Rosa gymnocarpa	Wild rose	1.8	9.3

Table 2.--(cont., page 3)

Plant species	Common name	Frequency	
		Riparian (n=280)	Upland (n=280)
Rubus spectabilis	Salmonberry	22.5	0.7
Rubus ursinus	Trailing blackberry	51.4	40.7
Vaccinium alaskaense	Alaska huckleberry	17.5	22.5
Vaccinium parvifolium	Red huckleberry	35.0	33.3

Chapter I

Table 3.--Mean percent cover (and standard error) and frequency of abundant tree species by habitat. T tests were used to document significant differences between riparian and upland habitat for mean percent cover (n=280).

	Mean percent cover		Frequency	
Tree species	Riparian	Upland	Riparian	Upland
Acer circinatum	17.7 (1.87)	6.9 (1.20)***	32.5	15.7
Acer macrophyllum	19.2 (1.89)	2.4 (0.62)***	64.6	9.3
Alnus rubra	16.1 (1.81)	0.3 (0.19)***	30.4	1.4
Cornus nuttalli	0.4 (0.31)	4.8 (0.97)***	1.1	11.8
Pseudotsuga menziesii	22.6 (1.78)	53.8 (2.20)***	56.1	87.1
Taxus brevifolia	2.7 (0.76)	4.1 (0.88)	7.5	9.6
Thuja plicata	4.1 (0.76)	4.3 (0.97)	12.5	8.6
Tsuga heterophylla	15.6 (1.75)	28.9 (2.18)***	34.3	46.8

Chapter I

Table 4.--Measures of vegetative diversity.

Diversity measure	Riparian	Upland
Foliage height diversity	4.64	4.05
Species richness	96	73
Species evenness	0.92	0.80
Species diversity	4.18	3.44
Maximum diversity	4.56	4.29

Table 5.--Designation and description of habitat variables used in the analysis.

Variable mnemonic	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 herbs
HERBEV	Percent cover of evergreen herbs
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 to nearest permanent water source (m)
FHD	Foliage height diversity, $1/\Sigma p_i^2$
SNAGNUM	Number of snags in 100 m^2
AVGLOGDI	Average diameter of logs in 100 m^2

Chapter I

Table 5.--(cont., p. 2)

Variable mnemonic	Description
NEWLOGS	Total length of recently fallen logs, decomposition classes 1 and 2
OLDLOGS	Total length of decayed logs, decomposition classes 3, 4 and 5
SLOPE	Average of upslope and downslope gradient

Chapter I

Table 6.--Mean ($\bar{X}$) and standard error (S.E.) for number of individuals per ha by habitat (n=41). T tests were used to document significant differences between riparian and upland habitat. **P*<0.05; ***P*<0.01; ****P*<0.001.

Species	Code name	Riparian $\bar{X}$	Riparian S.E.	Upland $\bar{X}$	Upland S.E.	
Order Insectivora						
Sorex vagrans	SOVA	0.1	0.07	0.0		
Sorex monticolus	SOMO	6.5	1.02	2.8	0.49	**
Sorex palustris	SOPA	0.1	0.05	0.0		
Sorex bendirii	SOBE	0.1	0.07	0.0		
Sorex trowbridgii	SOTR	7.3	1.17	5.7	0.85	
Neurotrichus gibbsii	NEGI	1.0	0.40	0.6	0.13	
Scapanus orarius	SCOR	0.5	0.14	0.6	0.21	
Order Rodentia						
Tamias townsendii	TATO	12.2	1.74	13.1	1.50	
Spermophilus beecheyi	SPBE	0.0		0.03		
Tamiasciurus douglasii	TADO	0.1	0.07	0.04	0.04	
Glaucomys sabrinus	GLSA	0.9	0.27	1.5	0.34	
Peromyscus maniculatus	PEMA	41.1	4.83	23.2	3.73	**
Neotoma cinerea	NECI	0.2	0.08	0.2	0.10	
Clethrionomys californicus	CLCA	2.4	0.69	7.3	0.76	***

Chapter I

Table 6.--(cont., p. 2)

		Riparian		Upland		
Species	Code name	$\bar{X}$	S.E.	$\bar{X}$	S.E.	
Order Rodentia (cont.)						
Microtus oregoni	MIOR	4.8	0.72	2.0	0.48	**
Microtus richardsoni	MIRI	1.1	0.30	0.0		***
Zapus trinotatus		7.0	1.44	1.7	0.53	**
Order Carnivora						
Mustela erminea		0.9	0.22	0.2	0.10	*
Mustela frenata		0.04		0.0		

Chapter I

Table 7.--Mean and minimum value for weight (in g) of animals in breeding condition by sex.

Species	Females			Males		
	n	Mean	Minimum	n	Mean	Minimum
Order Insectivora						
Sorex monticolus	24	8.58	6.50	73	8.35	4.25
Sorex bendirii	1	25.00		1	20.00	
Sorex trowbridgii	20	5.13	4.00	21	4.98	3.75
Neurotrichus gibsii	1	7.00		3	7.08	6.25
Scapanus orarius				1	74.75	
Order Rodentia						
Tamias townsendii	225	81.99	53.00	302	76.55	56.50
Tamiasciurus douglasii				1	125.00	
Glaucomys sabrinus	26	152.75	116.00	16	128.88	65.00
Peromyscus maniculatus	729	20.61	13.50	961	18.83	10.00
Neotoma cinerea	1	265.00				
Clethrionomys californicus	180	22.83	15.50	220	23.54	11.75
Microtus oregoni	59	17.68	11.00	84	21.21	13.00
Microtus richardsoni	24	77.83	66.00	20	89.42	50.00
Zapus trinotatus	140	29.73	19.50	162	22.97	14.25
Order Carnivora						
Mustela erminea	1	36.00				

Chapter I

Table 8.--Mean ($\bar{X}$) and standard error (*S.E.*) for weight (in g) of adults by habitat type. T tests were used to document significant differences between riparian and upland habitat. *$P<0.05$; **$P<0.01$; ***$P<0.001$.

	Riparian			Upland			
Species	*n*	$\bar{X}$	*S.E.*	*n*	$\bar{X}$	*S.E.*	
Order Insectivora							
Sorex vagrans	3	3.4	0.22				
Sorex monticolus	167	7.6	0.18	63	7.2	0.20	
Sorex palustris	2	10.0	0.50				
Sorex bendirii	2	22.5	2.50				
Sorex trowbridgii	188	4.6	0.05	136	4.5	0.04	
Neurotrichus gibbsii	25	8.5	0.20	16	8.1	0.21	
Scapanus orarius	16	53.1	1.96	14	51.2	2.05	
Order Rodentia							
Tamias townsendii	995	78.4	0.25	1081	77.5	0.25	*
Spermophilus beecheyi				1	387.0		
Glaucomys sabrinus	34	148.1	3.37	39	132.0	3.75	**
Peromyscus maniculatus	3009	17.8	0.07	1698	17.2	0.07	***
Neotoma cinerea	2	270.8	70.75	3	201.7	31.67	
Clethrionomys californicus	117	23.5	0.36	393	22.2	0.19	**
Microtus oregoni	231	18.5	0.26	66	17.3	0.26	**

Table 8.--(cont., p. 2)

Species	Riparian			Upland		
	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.
Order Rodentia (cont.)						
Microtus richardsoni	103	85.2	1.64			
Zapus trinotatus	348	25.8	0.28	69	25.6	0.59
Order Carnivora						
Mustela erminea	12	58.8	4.89	3	46.2	5.66

Chapter I

Table 9.--Mean (X̄) and standard error (S.E.) for biomass per ha by habitat (n=41). T tests were used to document significant differences between riparian and upland habitat. $*P<0.05$; $**P<0.01$; $***P<0.001$.

Species	Riparian X̄	Riparian S.E.	Upland X̄	Upland S.E.	
Order Insectivora					
Sorex vagrans	0.4	0.25	0.0		
Sorex monticolus	47.6	7.49	19.3	3.37	**
Sorex palustris	0.7	0.49	0.0		
Sorex bendirii	1.6	1.57	0.0		
Sorex trowbridgii	32.8	5.27	24.6	3.69	
Neurotrichus gibsii	8.9	3.40	4.9	1.06	
Scapanus orarius	29.1	7.64	28.2	10.38	
Order Rodentia					
Tamias townsendii	950.1	136.01	1006.7	115.58	
Spermophilus beecheyi	0.0		13.5		
Tamiasciurus douglasii	18.5	8.95	0.0		*
Glaucomys sabrinus	128.5	39.91	198.7	44.12	
Peromyscus maniculatus	721.8	84.82	389.9	62.65	**
Neotoma cinerea	44.8	21.65	33.4	16.69	

Table 9.--(cont., p. 2)

Species	Riparian		Upland		
	X̄	S.E.	X̄	S.E.	
Order Rodentia (cont.)					
Clethrionomys californicus	55.0	15.80	159.4	16.51	***
Microtus oregoni	87.9	13.11	33.9	8.13	***
Microtus richardsoni	87.0	24.03	0.0		***
Zapus trinotatus	177.5	36.40	42.0	13.12	**
Order Carnivora					
Mustela erminea	51.4	13.42	11.6	5.17	**
Mustela frenata	2.6		0.0		

Chapter I

Table 10.--Mean ($\bar{X}$) and standard error (*S.E.*) for minimum survival time by habitat. Values do not include single captures of individuals. Statistical comprisons between riparian and upland habitat were assessed using t tests. None of the values were statistically significant.

	Riparian			Upland		
Species	*n*	$\bar{X}$	*S.E.*	*n*	$\bar{X}$	*S.E.*
Order Insectivora						
Sorex monticolus	32	99.8	39.06	9	187.9	69.22
Sorex trowbridgii	13	65.9	18.87	7	43.1	10.37
Neurotrichus gibbsii				1	12.0	
Scapanus orarius	3	53.7	19.19	3	144.7	117.25
Order Rodentia						
Tamias townsendii	114	90.3	12.50	120	90.2	12.17
Glaucomys sabrinus	6	23.7	9.90	10	54.5	36.39
Peromyscus maniculatus	355	72.5	5.51	210	59.3	5.15
Neotoma cinerea	1	59.0		1	5.0	
Clethrionomys californicus	23	71.0	25.17	68	66.9	14.01
Microtus oregoni	38	66.9	18.68	19	40.8	16.42
Microtus richardsoni	13	80.5	31.74			
Zapus trinotatus	77	77.0	14.49	16	76.9	32.11
Order Carnivora						
Mustela erminea	3	25.7	15.19			

Table 11.--First and final dates (and duration of breeding season in days) for captures of males in breeding condition.

Species	1981		1982		1983	
	Riparian	Upland	Riparian	Upland	Riparian	Upland
Order Insectivora						
Sorex monticolus	Jul 30-Oct 25(88)	Aug 11-Aug 31(21)	Jun 29-Nov 14(139)	Jul 27-Jul 30(4)	Jun 22-Oct 1(102)	Jun 22-Nov 14(146)
Sorex bendirii			Jul 10-Jul 10(1)			
Sorex trowbridgii	Aug 7-Sep 22(47)	Jul 30-Jul 30(1)	Jul 10-Oct 4(87)	Jul 25-Sep 24(62)	Jun 28-Jun 28(1)	Aug 31-Oct 26(57)
Neurotrichus gibbsii	Aug 28-Aug 29(2)	Aug 29-Aug 29(1)				
Scapanus orarius		Aug 31-Aug 31(1)				
Order Rodentia						
Tamias townsendii	Aug 5-Sep 19(46)	Aug 8-Sep 18(42)	Jun 25-Nov 15(144)	Jun 25-Nov 12(141)	Jun 22-Jun 29(8)	Jun 21-Jun 29(9)
Tamiasciurus douglasii		Aug 8-Aug 8(1)	Nov 7-Nov 7(1)			
Glaucomys sabrinus	Oct 10-Oct 10(1)	Aug 31-Sep 20(21)	Jul 24-Nov 11(111)	Jul 3-Jul 3(1)	Jun 23-Aug 18(57)	Jun 21-Jun 29(9)
Peromyscus maniculatus	Jul 21-Oct 6(78)	Jun 23-Oct 7(127)	Jun 25-Nov 15(144)	Jul 12-Nov 13(125)	Jun 21-Nov 2(135)	Jun 21-Nov 1(134)
Neotoma cinerea	Sep 6-Sep 6(1)	Aug 10-Aug 10(1)				
Clethrionomys californicus	Aug 6-Oct 5(61)	Jul 31-Oct 25(87)	Jun 26-Oct 27(124)	Jun 26-Oct 23(120)	Aug 17-Aug 22(6)	Jun 22-Nov 13(145)
Microtus oregoni	Jul 31-Sep 8(40)	Aug 20-Sep 19(31)	Jul 3-Nov 13(134)	Jul 17-Oct 6(82)	Jul 7-Oct 28(114)	Sep 17-Sep 17(1)
Microtus richardsoni	Aug 21-Sep 7(18)		Jul 26-Jul 26(1)		Aug 4-Sep 21(49)	
Zapus trinotatus	Aug 5-Sep 19(46)	Sep 22-Sep 23(2)	Jun 25-Nov 14(143)	Jun 29-Sep 20(84)	Jun 21-Jul 10(20)	Jun 21-Jul 14(24)

Table 12.--First and final dates (and duration of breeding season in days) for captures of females in breeding condition.

	1981		1982		1983	
Species	Riparian	Upland	Riparian	Upland	Riparian	Upland
Order Insectivora						
Sorex monticolus			Jun 30-Nov 8(132)	Jun 26-Aug 8(44)	Jun 24-Aug 22(60)	Aug 7-Sep 19(44)
Sorex bendirii			Jul 10-Jul 10(1)			
Sorex trowbridgii	Aug 10-Aug 10(1)		Jun 26-Oct 3(100)	Jun 28-Oct 11(106)	Jun 21-Jun 21(1)	Jun 21-Sep 27(99)
Neurotrichus gibbsii			Jun 28-Jun 28(1)			
Order Rodentia						
Tamias townsendii	Aug 7-Oct 4(59)	Aug 21-Sep 9(20)	Jun 25-Oct 22(120)	Jun 25-Oct6 28(126)	Jun 21-Oct 18(120)	Jun 21-Oct 19(121)
Glaucomys sabrinus		Aug 9-Sep 23(47)	Jun 25-Jul 2(8)	Jun 29-Oct 4(98)	Jun 24-Sep 1(70)	Aug 18-Aug 19(2)
Peromyscus maniculatus	Jul 22-Oct 13(84)	Jul 24-Oct 11(84)	Jun 25-Nov 15(144)	Jul 11-Nov 15(128)	Jun 21-Nov 9(142)	Jun 21-Nov 16(149)
Neotoma cinerea				Sep 25-Sep 25(1)		
Clethrionomys californicus	Sep 7-Oct 3(27)	Aug 7-Nov 1(87)	Jun 25-Oct 26(124)	Jun 25-Oct 29(127)	Jun 21-Nov 14(147)	Jun 21-Oct 26(128)
Microtus oregoni	Aug 6-Sep 22(48)	Aug 29-Sep 18(21)	Jul 2-Oct 11(102)	Jun 28-Sep 24(90)	Jul 8-Oct 4(89)	Aug 30-Aug 30(1)
Microtus richardsoni			Jun 25-Oct 29(127)		Aug 16-Sep 21(37)	
Zapus trinotatus	Sep 5-Sep 5(1)		Jun 27-Oct 11(107)	Jun 29-Oct 10(104)	Jun 21-Sep 15(87)	Jun 27-Jul 14(17)
Order Carnivora						
Mustela erminea			Jul 15-Jul 15(1)			

Table 13.--Percent of juveniles by habitat.

Species	Riparian		Upland	
	n	Percent	n	Percent
Order Insectivora				
Sorex monticolus	203	17.7	83	24.1
Sorex trowbridgii	201	6.5	154	11.7
Neurotrichus gibbsii	21	3.8	16	0.0
Scapanus orarius	16	0.0	17	17.6
Order Rodentia				
Tamias townsendii	1014	1.9	1106	2.3
Tamiasciurus douglasii	4	100.0	1	100.0
Glaucomys sabrinus	36	5.6	49	20.4
Peromyscus maniculatus	3140	4.2	1827	7.1
Neotoma cinerea	7	71.4	8	62.5
Clethrionomys californicus	124	5.6	408	3.7
Microtus oregoni	238	2.9	68	2.9
Microtus richardsoni	119	13.5		
Zapus trinotatus	365	4.7	75	8.0
Order Carnivora				
Mustela erminea	25	52.0	6	50.0
Mustela frenata	1	100.0		

Table 14.--Correlations between small mammals and habitat variables (n=560). Value represents significant Spearman's rank correlation coefficient ($P<0.01$). Plus or minus sign indicates direction of nonsignificant correlation. * $P<0.01$; ** $P<0.001$ Variable mnemonics follow those outlined in Table 1.

Species	Stratnum	Specnum	Soilex	Rock	Leaflt	Lichen	Moss	Herbdc	Herbev	Shrubdc	Shrubev	Treedc	Treeev	Creekdis	FHD	Snagnum	Avglogdi	Newlogs	Oldlogs	Slope
Order Insectivora																				
Sorex																				
monticolus	0.11*	+	+	+	-	-0.13*	-0.12*	0.17**	0.13*	0.11*	-0.24**	0.16**	-0.16**	-0.16**	-	-	+	+	+	-
Sorex																				
trowbridgii	+	-	-	+	-	-0.15**	+	+	+	-	-0.12*	0.16**	+	-	-	-	-	-	+	-
Neurotichus																				
gibbsii	+	-	+	-	-	-0.12*	-	+	+	+	-	+	-	+	-	-0.13*	-	-	+	-
Scapanus																				
orarius	+	+	+	+	+	-	-	+	-	+	-	+	-	+	-	-	-	-	-	-
Order Rodentia																				
Tamias																				
townsendii	-0.15**	+	-0.18**	-	-	0.29**	-	-0.12*	0.14**	+	0.15**	-0.31**	0.17**	+	+	0.25**	0.20**	+	0.21**	0.15**
Glaucomys																				
sabrinus	-	+	-	-	-	+	+	-0.17**	-	-	0.17**	-0.17**	0.15**	+	-	+	+	-	+	0.22**

Table 14.--(cont., p. 2)

Species	Stratnum	Specnum	Soilex	Rock	Leaflt	Lichen	Moss	Herbdc	Herbev	Shrubdc	Shrubev	Treedc	Treeev	Creekdis	FHD	Snagnum	Avglogdi	Newlogs	Oldlogs	Slope
Order Rodentia (cont.)																				
Peromyscus																				
maniculatus	-	0.32**	-	0.22**	-0.19**	0.19**	-	0.23**	+	0.19**	-0.31**	-	-0.11*	-0.40**	-	+	0.13*	-	0.13*	-0.19**
Neotoma																				
cinerea	-	-	-	-	+	+	+	-	-	-	-	+	+	-	+	-	+	-	+	-
Clethrionomys																				
californicus	-0.16**	+	-0.16**	-	-0.11*	0.22**	0.12*	-	-	-	0.25**	-0.36**	0.25**	0.24**	-0.13*	0.12*	+	+	+	+
Microtus																				
oregoni	0.18**	+	+	+	+	-	-	0.31**	0.14**	0.16**	-0.20**	0.11*	-	-0.13*	-	-	-	-	-	-0.12*
Microtus																				
richardsoni	+	0.22**	+	0.15**	-0.11*	-	-	0.20**	-	0.17**	-0.19**	+	-0.24**	-0.34**	+	-	-	0.12*	+	-0.21**
Zapus																				
trinotatus	0.12*	0.28**	-	+	-	+	-0.20**	0.29**	+	0.27**	-0.27**	0.16**	-0.39**	-0.44**	0.13**	+	+	+	+	-0.18**
Order Carnivora																				
Mustela																				
erminea	-	+	-	+	+	-	-	+	0.11*	+	-0.11*	+	-	-	-	+	+	+	+	-

Table 15.--Diversity measures (and standard error) for small mammal community by habitat. T tests were used to document significant differences between riparian and upland habitat for the diversity index and evenness index. Sample sizes are as follows: for 1981, n=15; for 1982, n=16; for 1983, n=20. ***P*<0.01.

	1981		1982		1983	
Diversity measure	Riparian	Upland	Riparian	Upland	Riparian	Upland
Species richness	16	13	16	12	12	12
No. of individuals	412	297	569	340	526	359
Mean diversity index	1.30(0.08)	1.50(0.06)	1.34(0.07)	1.30(0.09)	1.62(0.06)	1.55(0.08)
Maximum diversity	2.77	2.56	2.77	2.49	2.48	2.48
Mean evenness index	0.63(0.04)	0.79(0.03)**	0.63(0.03)	0.66(0.04)	0.80(0.02)	0.84(0.02)

Fig. 1.1.--Average monthly values for maximum air temperature for 1982 and 1983. Data was recorded with thermographs stationed in the riparian and upland grids at the Upper Lookout site. Data was provided by the Andrews Metereological Network.

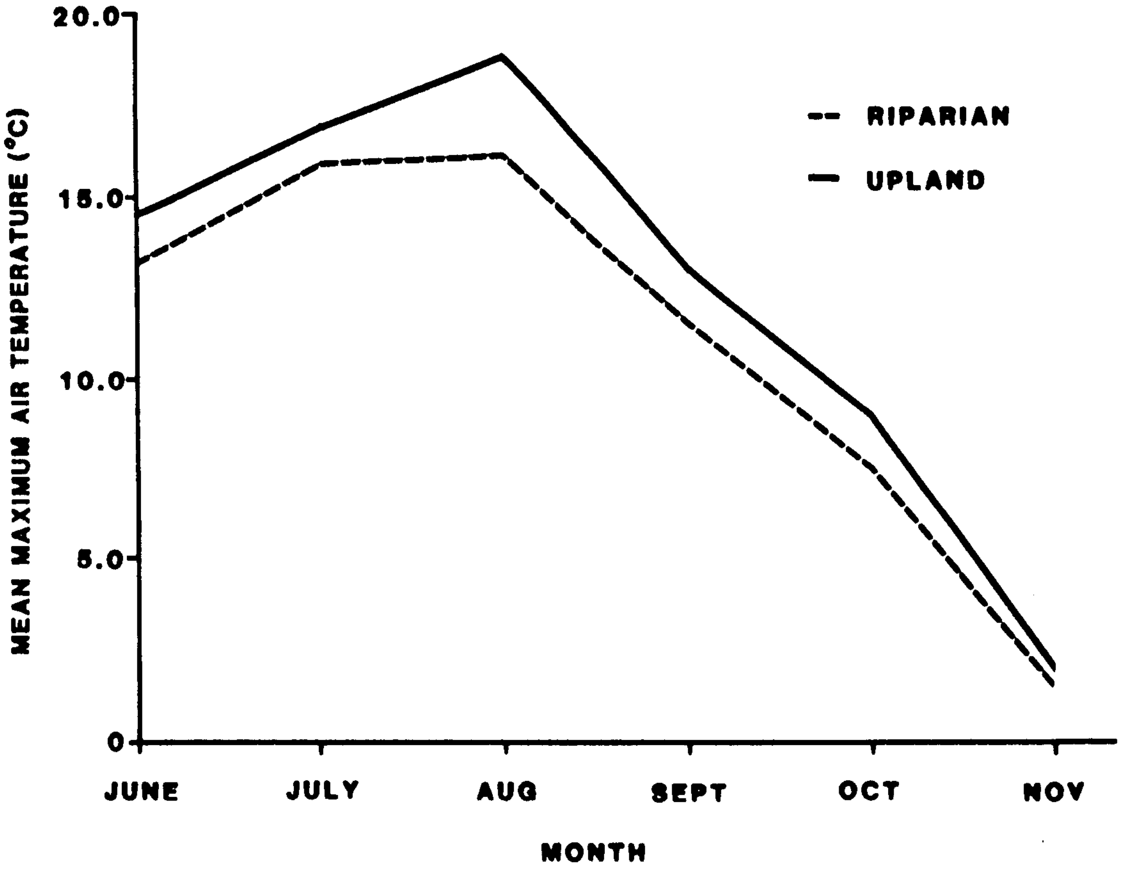
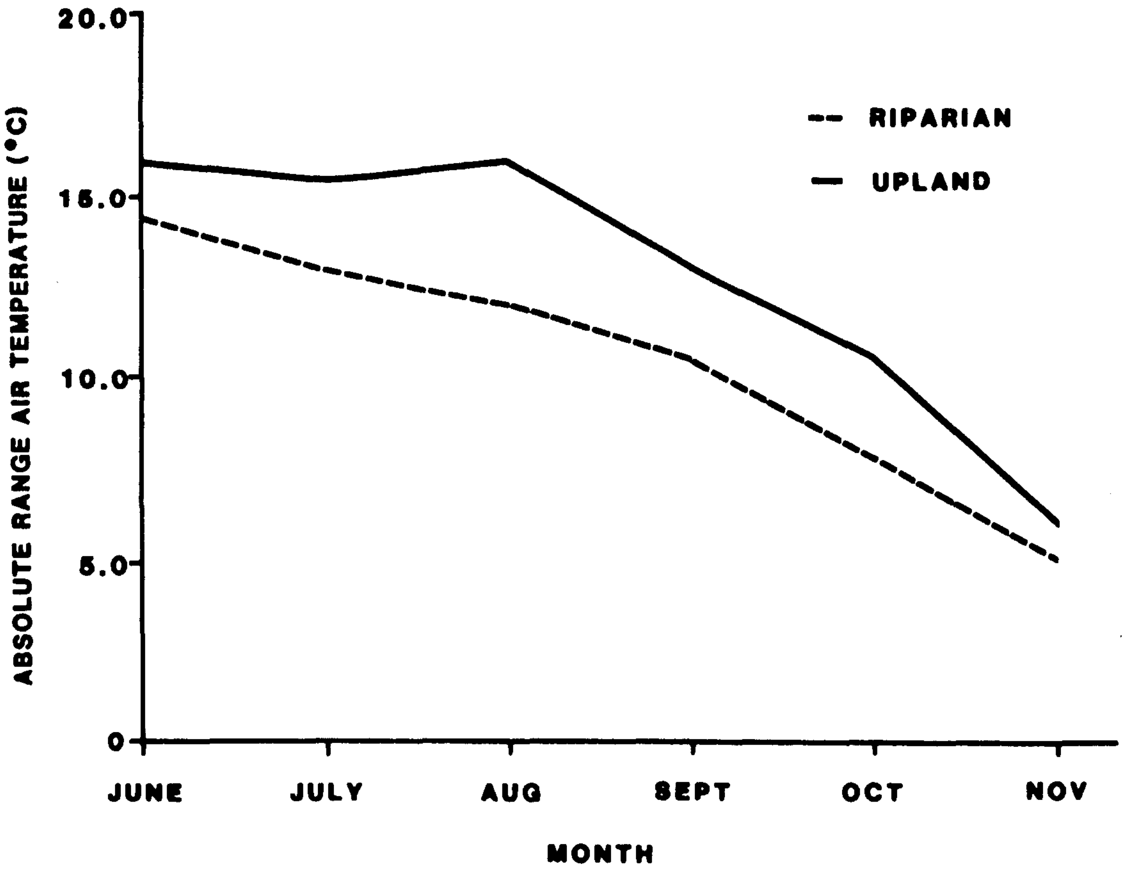

20.0
15.0
10.0
5.0
0
MEAN MAXIMUM AIR TEMPERATURE (°C)
-- RIPARIAN
— UPLAND
JUNE
JULY
AUG
SEPT
OCT
NOV
MONTH

Fig. 1.1.

Fig. 1.2.--Average monthly values for the absolute range of air temperatures for 1982 and 1983. Data was recorded with thermographs stationed in the riparian and upland grids at the Upper Lookout site. Data was provided by the Andrews Metereological network.



20.0
15.0
10.0
5.0
0
ABSOLUTE RANGE AIR TEMPERATURE (°C)
RIPARIAN
UPLAND
JUNE
JULY
AUG
SEPT
OCT
NOV
MONTH

Fig. 1.2.

Fig. 1.3.--Frequency of captures of species in the orders Insectivora and Carnivora by habitat type. Trap effort was equivalent in riparian and upland habitats. Species mnemonics follow those outlined in Table 7.

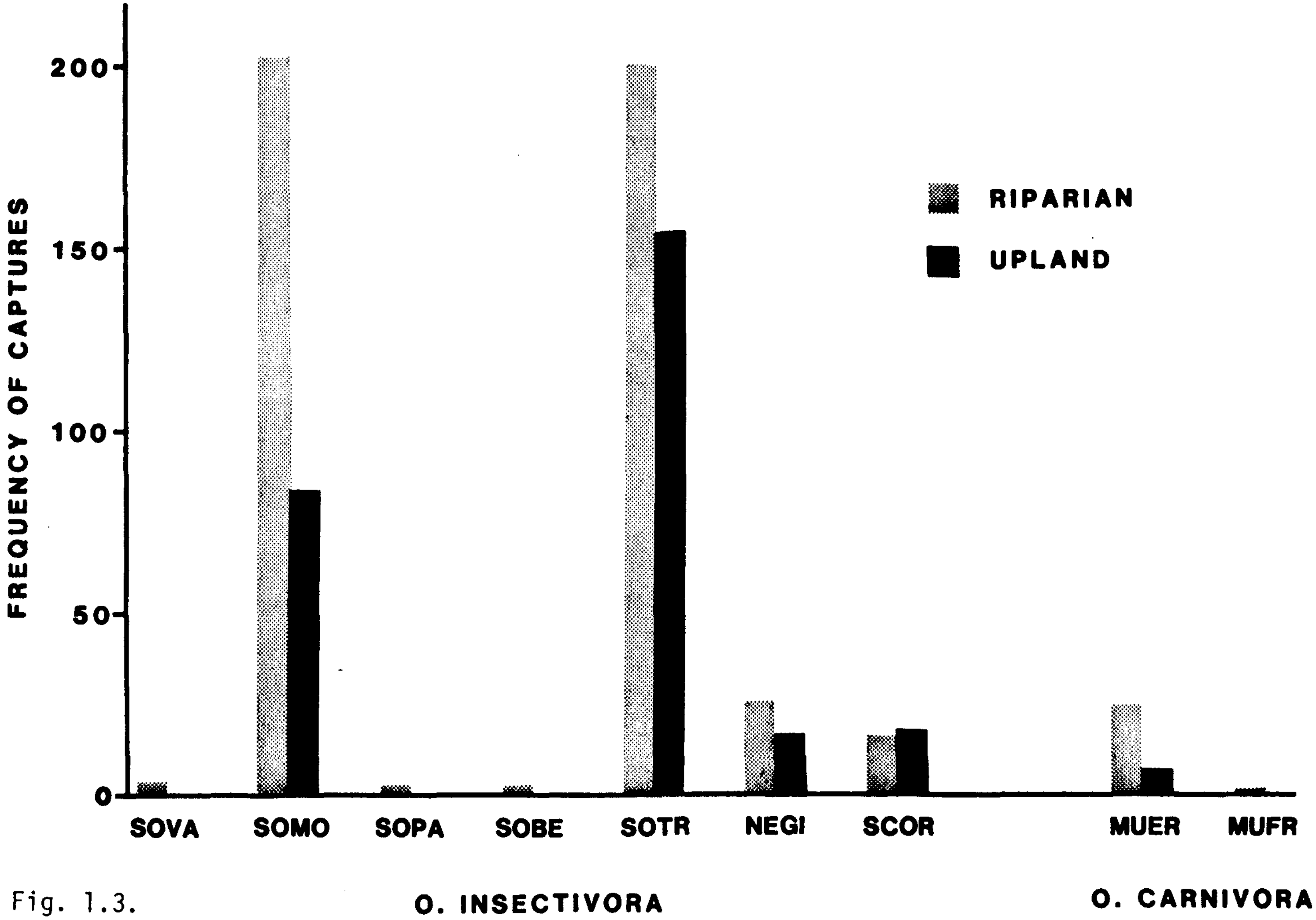

RIPARIAN
UPLAND
FREQUENCY OF CAPTURES
200
150
100
50
0
SOVA
SOMO
SOPA
SOBE
SOTR
NEGI
SCOR
MUER
MUFR
O. INSECTIVORA
O. CARNIVORA

Fig. 1.3.

Fig. 1.4.--Percent of adult males in breeding condition for species in the order Insectivora by habitat type. Values above bars represent the number of observations that percentage is based on. Species mnemonics follow those outlined in Table 7.

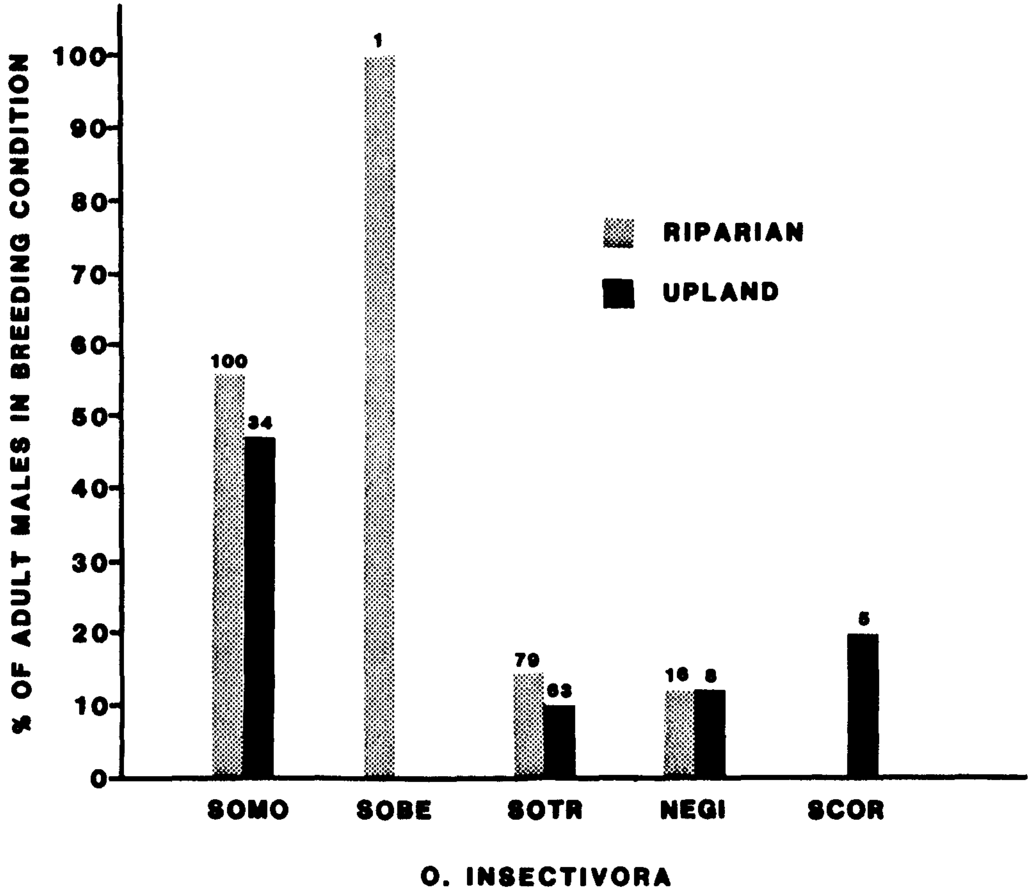

% OF ADULT MALES IN BREEDING CONDITION
0
10
20
30
40
50
60
70
80
90
100
RIPARIAN
UPLAND
100
34
1
79
63
16
8
5
SOMO
SOBE
SOTR
NEGI
SCOR
O. INSECTIVORA

Fig. 1.4.

Fig. 1.5.--Percent of adult females in breeding condition for species in the orders Insectivora and Carnivora by habitat type. Values above bars represent the number of observations that percentage is based on. Species mnemonics follow those outlined in Table 7.

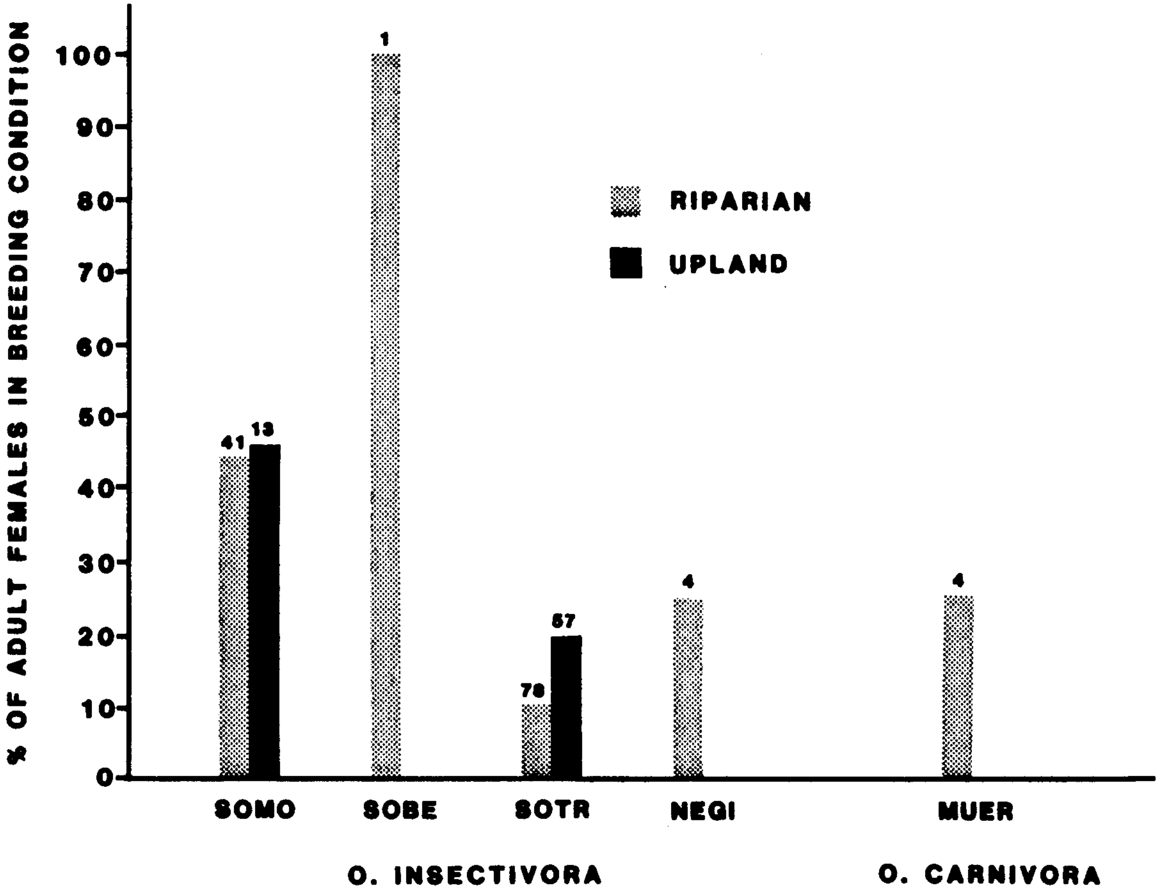

% OF ADULT FEMALES IN BREEDING CONDITION
0
10
20
30
40
50
60
70
80
90
100
RIPARIAN
UPLAND
41
13
1
78
57
4
4
SOMO
SOBE
SOTR
NEGI
MUER
O. INSECTIVORA
O. CARNIVORA

Fig. 1.5.

Fig. 1.6.--Frequency of captures of species in the order Rodentia by habitat type. Trap effort was equivalent in riparian and upland habitats. Species mnemonics follow those outlined in Table 7.

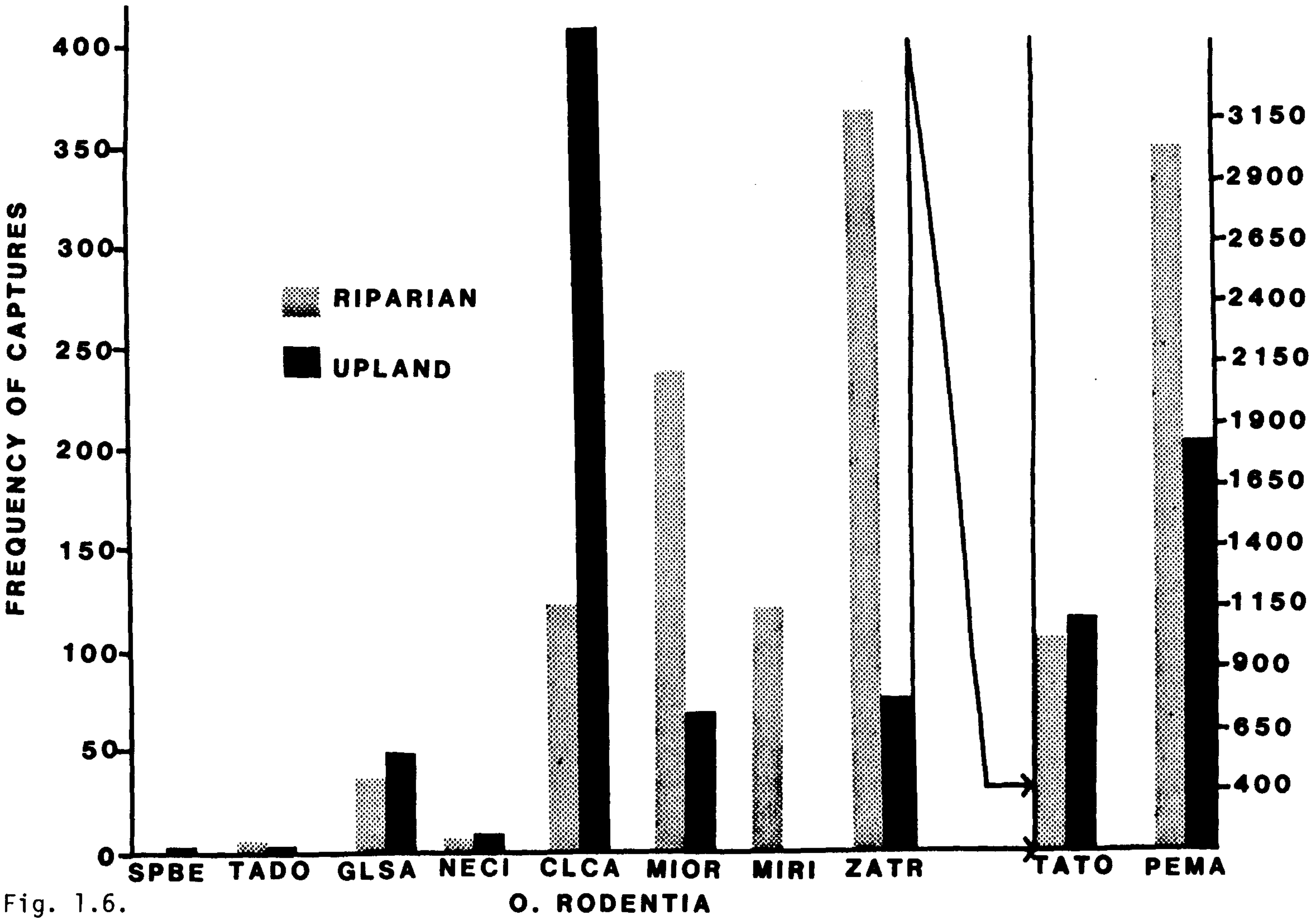
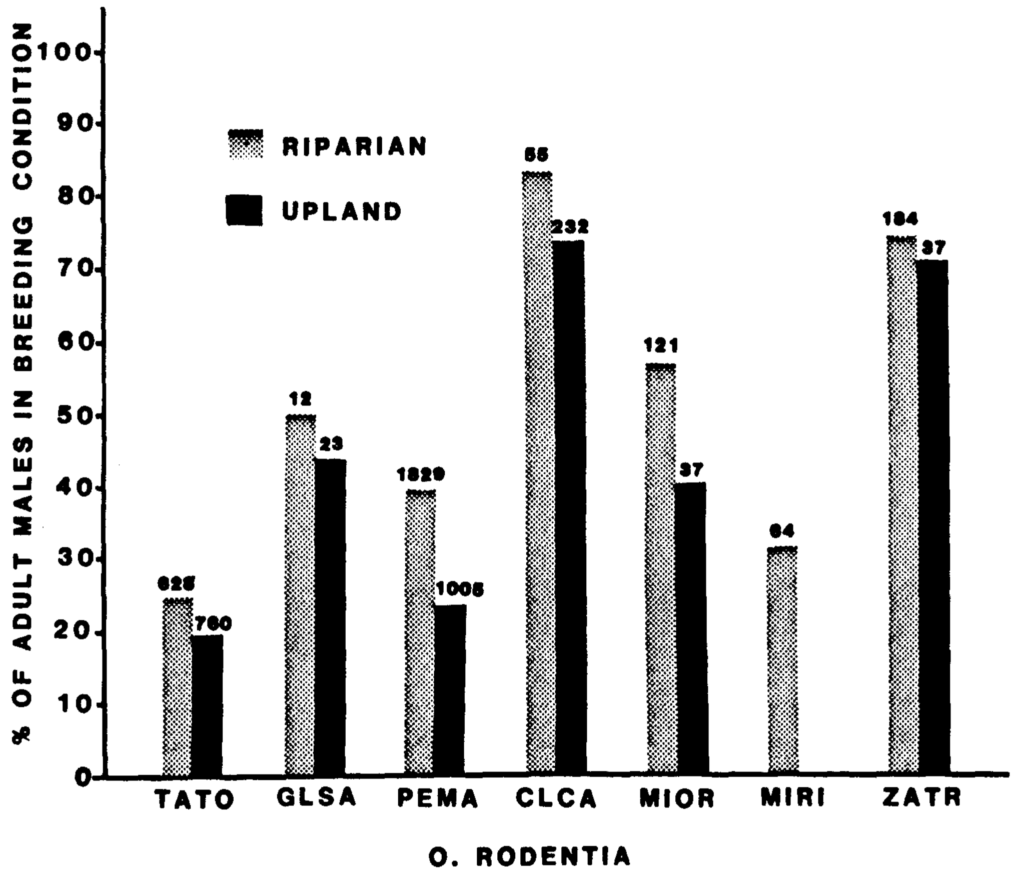

FREQUENCY OF CAPTURES
400
350
300
250
200
150
100
50
0
RIPARIAN
UPLAND
3150
2900
2650
2400
2150
1900
1650
1400
1150
900
650
400
SPBE
TADO
GLSA
NECI
CLCA
MIOR
MIRI
ZATR
TATO
PEMA
O. RODENTIA

Fig. 1.6.

Fig. 1.7.--Percent of adult males in breeding condition for species in the order Rodentia by habitat type. Values above bars represent the number of observations that percentage is based on. Species mnemonics follow those outlined in Table 7.



% OF ADULT MALES IN BREEDING CONDITION
100
90
80
70
60
50
40
30
20
10
0
▨ RIPARIAN
■ UPLAND
625
760
12
23
1829
1005
55
232
121
37
64
184
37
TATO
GLSA
PEMA
CLCA
MIOR
MIRI
ZATR
O. RODENTIA

Fig. 1.7.

Fig. 1.8.--Percent of adult females in breeding condition for species in the order Rodentia by habitat type. Values above bars represent the number of observations that percentage is based on. Species mnemonics follow those outlined in Table 7.

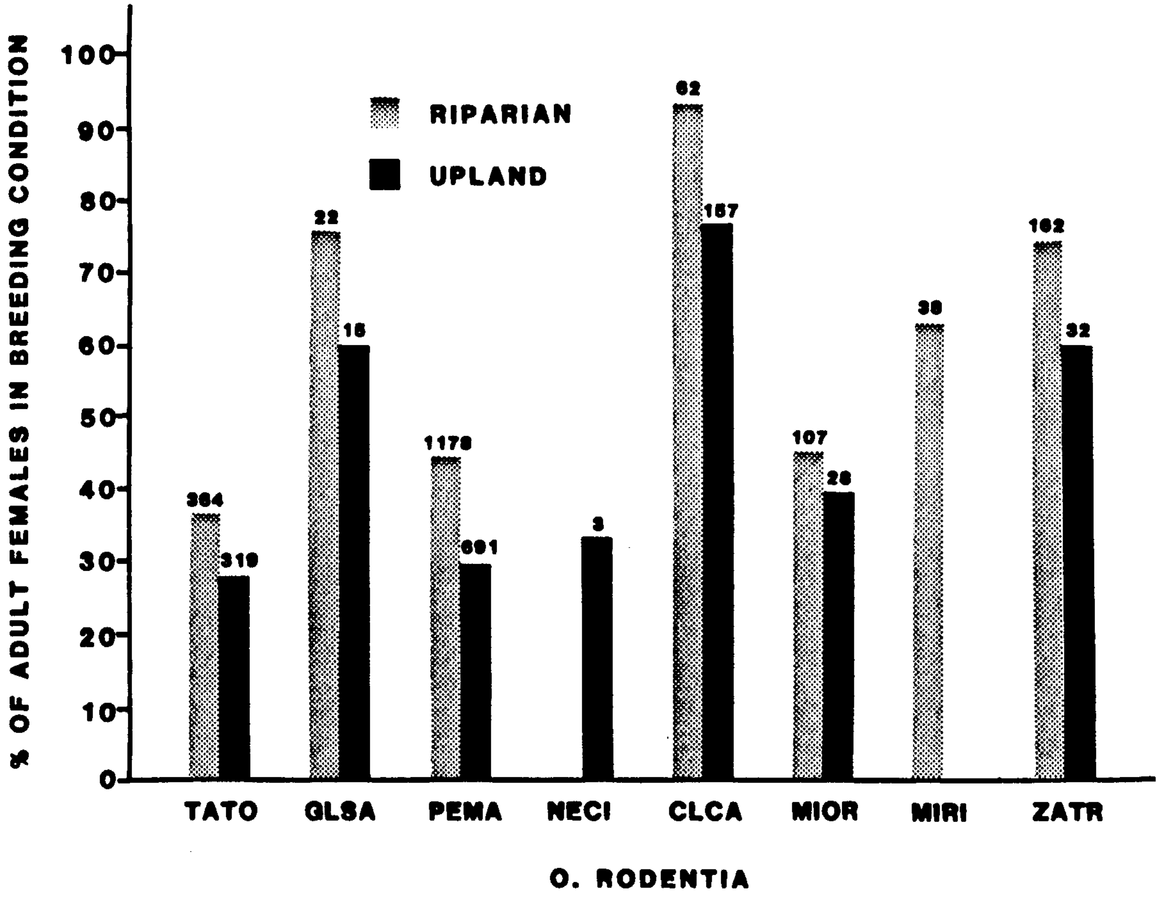

% OF ADULT FEMALES IN BREEDING CONDITION
0
10
20
30
40
50
60
70
80
90
100
RIPARIAN
UPLAND
364
319
22
15
1178
691
3
62
157
107
28
38
162
32
TATO
GLSA
PEMA
NECI
CLCA
MIOR
MIRI
ZATR
O. RODENTIA

Fig. 1.8.

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CHAPTER II

MICROHABITAT SEPARATION BETWEEN SYMPATRIC MICROTINES, *CLETHRIONOMYS CALIFORNICUS*, *MICROTUS OREGONI*, AND *M. RICHARDSONI*

ABSTRACT

This study examined microhabitat separation between three sympatric species of voles (subfamily Microtinae): *Microtus oregoni*, *M. richardsoni*, and *Clethrionomys californicus*. These species were selected for studying microhabitat separation because they are potential competitors due to similarities 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. The habitat around each of 560 trap stations was analyzed. Discriminant function analysis distinguished between microhabitats used by a species vs. microhabitats that were available but were not used. *C. californicus* selected microhabitats with a high percent cover of lichen and western hemlock and a low percent cover of deciduous trees. *M. oregoni* selected microhabitats high in herbaceous vegetation (both deciduous and evergreen) and high in deciduous shrubs. Those microhabitats selected by *M. richardsoni* had a high soil exposure, high total length of recently fallen

logs, and low canopy cover of Douglas-fir. Combining the three microtine species in one discriminant procedure identified variables effective in distinguishing between species microhabitats. These variables were percent cover of lichen, canopy cover of deciduous trees, and distance from the creek.

INTRODUCTION

Small mammal distribution and diversity is influenced by many factors including structural habitat suitability, intra- and interspecific competition, and the distribution and abundance of food (Brown, 1973; Brown and Lieberman, 1973; Dueser and Shugart, 1978 O'Farrell, 1980; Rosenzweig and Winakur, 1969). The mechanisms for species coexistence include partitioning food resources (Brown, 1973; Brown and Lieberman, 1973), arboreal habitat separation (Holbrook, 1979b), and variation in daily and seasonal activity patterns (Glass and Slade, 1980; M'Closkey, 1976; O'Farrell, 1974, 1980). Species coexistence may also be maintained by microhabitat separation (Dueser and Shugart, 1978, 1979; Holbrook, 1979a, 1979b; M'Closkey, 1976; M'Closkey and Fieldwick, 1975; Morris, 1979; Rosenzweig and Winakur, 1969). Many studies attempting to analyze patterns of small mammal species distributions have been conducted with heteromyid rodents in arid environments (Brown, 1973; Brown and Lieberman, 1973; Rosenzweig and Sterner, 1970; Rosenzweig and Winakur, 1969; Whitford, 1976). These studies suggest that the coexistence of heteromyid species is a function of habitat complexity, amount of annual rainfall, and the ability to partition seed resources. In the desert, seeds provide a year-round particulate resource that can be partitioned along a size gradient. Because seeds are not available on a year-round basis in the coniferous forests of the

Pacific Northwest, we would expect other resources to be important dimensions on which ecologically similar species segregate.

Microhabitat separation of *Clethrionomys californicus*, *Microtus oregoni*, and *M. richardsoni* was studied because these species are potential competitors due to similarities in morphology and life history patterns. They are all herbivores; *C. californicus* feeds principally on lichens and subterranean fungi. Forbs and seeds are also included in the diet (Maser et al., 1981). *M. oregoni* feeds primarily on grasses, forbs, huckleberries (*Vaccinium* spp.), and substantial amounts of subterranean fungi (Maser et al., 1981). *M. richardsoni* feeds on forbs and huckleberries (Maser and Storm, 1970). All three species are primarily nocturnal (Maser et al., 1981) and are active throughout the year (Johnson and Johnson, 1982). They are all primarily subterrestrial (Maser et al., 1981) and share a similar morphology (Johnson and Johnson, 1982) and close phylogenetic relationship (Nadler et al., 1978).

To investigate how an assemblage of such similar species could coexist, I used discriminant function analysis to evaluate the significance of microhabitat separation and to determine which habitat variables were important in describing microhabitat differences. Specifically, this study addressed the following questions: 1) Are there structural differences among the microhabitats of three locally sympatric microtines? 2) What habitat variables describe these differences? 3) How do patterns of microhabitat selection relate to the availability of microhabitats? 4) What are the spatial distribution patterns between the vole species?

METHODS

Study area

Field research was conducted in the western Cascade Mountain Range near Blue River, Oregon (approximately 75 km east of Eugene, Oregon). This area is characterized by well-defined drainages and steep slopes. Soil is primarily a clay loam, volcanic in origin (Gashwiler, 1972). Bedrock is comprised of the Oligocene-Miocene Western Cascade Group (Franklin and Dyrness, 1971).

Annual precipitation ranges from 2,300 mm to 2,800 mm, 90% of which falls between October and April (Franklin and Dyrness, 1971). Above 900 m, snowpacks accumulate to 1 m or more. Temperatures are moderate with a mean July maximum of 29^{0}C and mean January minimum of -3^{0}C. A more complete description of the soils, climate, and bedrock can be found in Franklin and Dyrness (1971).

Four study sites were selected: two along Lookout Creek, a fourth order (Strahler, 1957) stream on the H.J. Andrews Experimental Forest; one along Hagan Creek, a fourth order stream in the Hagan Research Natural Area; and one along Marten Creek, a fifth order stream in the Eugene District of the Bureau of Land Management. The Upper and Lower Lookout sites are old-growth stands, approximately 250 years old. Hagan and Marten are mature forest stands, approximately 100 years old. Study sites were separated by a distance of at least 2.8 km.

Douglas-fir (Pseudotsuga menziesii) represents the most abundant conifer on the study sites. Other conifers include western hemlock (Tsuga heterophylla), western red cedar (Thuja plicata), silver fir (Abies amabilis), grand fir (Abies grandis), and Pacific yew (Taxus brevifolia). The primary deciduous trees are big-leaf maple (Acer macrophyllum), red alder (Alnus rubra), and vine maple (Acer circinatum). The predominant ground cover includes salal (Gaultheria shallon), western swordfern (Polystichum munitum), Oregon grape (Berberis nervosa), and Oregon oxalis (Oxalis oregona).

Trapping procedure

Trapping was conducted during the months of July through November of 1981 and June through November of 1982 and 1983. This time period represented a trap effort of 40,152 trap nights. At each of the four sites, two trapping grids were established, one in riparian habitat and one in nearby upland habitat. The vegetation and microclimate of riparian habitats are influenced by streams and their associated high water tables (USDI, 1980). Consequently, riparian habitat consists of moisture-dependent or at least moisture-tolerant plants. In the western Cascade Range, these plants are bigleaf maple, red alder, western swordfern, Oregon oxalis, maidenhair fern (Adiantum pedatum), and lady fern

(Athyrium felix-femina). The edge of the riparian habitat was identified by a change in plant species composition and relative abundance; the downslope boundary was the water's edge at low flow. The riparian grid was established randomly within the constraint that the grid was oriented perpendicular to the stream to maximize the stream/grid interface.

Due to the high precipitation in western Oregon, there is a large transition zone between the riparian and upland habitat. Farther away from the stream, the vegetation of the transition zone becomes more xeric and contains increasing quantities of Oregon grape, salal, and bracken fern (Pteridium aquilinum). The upland grids were placed upslope from the riparian grids beyond the transition zone. These grids were established fully within upland habitat as defined by the more xeric, predominantly coniferous community. The riparian and upland grids at a given site were separated from one another by approximately 150 m, depending on the width of the transition zone.

In 1981, each grid consisted of 56 trap stations. During 1982 and 1983 each grid was expanded to 70 trap stations. All grids had a grid interval of 10 m. Because of the linearity of the riparian habitat, the Upper Lookout riparian grid was 2 x 35 stations. All other grids were 7 x 10. One large Sherman live trap (8 by 9 by 23 cm) was placed at each trap station and was baited with a mixture of whole oats and sunflower seeds. Whole oats were used in preference to rolled oats because they retained their consistency during inclement weather. This bait was selected to minimize attraction of individuals from outside the sampling area. Livetrapping was conducted to avoid creating a vacuum that could attract individuals from outside the sampling area. Unbaited, unset traps were positioned at the trap stations for at least one week prior to trapping to minimize a neophobic reaction to the traps. Traps were set lightly to effectively sample juveniles as well as adults.

Within a 1 m radius of the grid coordinate, traps were placed at the base of a large log when available, and otherwise at the base of a stump, snag, or tree. In the absence of these structural components, traps were placed under the greatest amount of shrub or herbaceous cover. In each case, evidence of runways or burrowing activities directed trap placement. Traps were checked each morning as soon as light was sufficient to process mammals. Species, sex, age class, weight, and reproductive condition were noted. Each animal was marked by toe clipping prior to release at the capture site.

Habitat variables

The habitat around each of the 560 trap stations was analyzed. Criteria for selecting habitat variables and corresponding measurements were 1) suspected relevance to microhabitat distribution, 2) ability to be quickly and accurately measured with minimal disturbance (due to the long-term nature of the study), and 3) repeatability.

There were two levels of habitat analysis around each trap station. Trees, logs, and snags were characterized in a 100 m^2-area centered around each trap. Tree measurements included density, height, DBH (diameter at breast height), and canopy cover by species, as well as canopy cover of all trees. Logs were measured for length and maximum diameter then classified according to a five-class decay scale described by Franklin et al. (1981). Snags were measured for height and DBH then classified on a five-class decay scale based on the texture of exposed wood and the presence of bark, twigs, and large branches.

Centered within each 100 m^2-plot was a 9 m^2-plot within which herbs and shrubs were characterized. The method of vegetative analysis was modified from Mueller-Dombois and Ellenberg (1974). Percent cover was recorded for each vegetative stratum. Plant species were listed and grouped with respect to stratum. Each species received a rating according to six cover classes: less than 5, 5 to less than 25, 25 to less than 50, 50 to less than 75, 75 to less than 95, and 95 to 100% (Daubenmire, 1968). Class midpoint values were used in calculations. Also measured were the number of vegetative strata that exceeded 15% cover, plant species richness, slope gradient, distance to the creek, and percent of exposed soil, and rock, leaf litter, moss, and lichen. Deciduous and evergreen components were measured for each vegetative stratum.

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. The quantity of vegetation per layer was converted to the proportion within each layer. Foliage height diversity was then calculated as $1/\Sigma\ p_i^2$ where p_i is the proportion of vegetation in the i^{th} layer to reflect the relative contribution of vegetation at varying heights to the total quantity of vegetation.

The subset of variables used in the analyses are listed in Table 1. Several additional variables were measured but were excluded from the analyses because of high intercorrelations ($\underline{r}$ >0.70) with other habitat variables. Combinations of variables that incorporated the same original data were avoided. Habitat analysis was conducted during the summer of 1981 and the summer of 1982.

Data analysis

Discriminant function analysis was used to compare microhabitats selected vs. those available (but not selected) and to compare patterns of microhabitat selection between the three species. This procedure maximizes among-group variation relative to within-group variation and extracts orthogonal functions most capable of separating the groups (Klecka, 1980). Total structure coefficients were used to assess the relative contribution of the habitat variables to the discriminant function. The total structure coefficient is the correlation of the original variable to the discriminant function and is considered more appropriate than either the unstandardized or the standardized canonical coefficient because interpretation is not influenced by intercorrelations between habitat variables (Klecka, 1980; Williams, 1983).

To assess the adequacy of the discriminant function, the original observations were classified to determine how many were correctly classified by the variables in the discriminant function. This procedure produces a probability of membership, then each observation is assigned to the group with the highest probability (Klecka, 1975).

For the discriminant analysis, the presence or absence of a microtine species at a trap station was associated with the corresponding microhabitat variables at that trap station. Therefore, the habitat variables at a given trap station were used only once in the data set to calculate value for microhabitats in which a species was caught. The discriminant analysis was based on 1982 trapping data since all trap stations had an equivalent effort during this year. Because the procedure was based on presence/absence of a species at a trap station, the use of an unequal trapping effort would have resulted in an unquantifiable bias. Stepwise discriminant analysis was run with BMDP statistical software (Dixon, 1983). Data from the eight trapping grids were pooled to yield information regarding patterns of microtine microhabitat utilization.

One of the assumptions of discriminant analysis is that the groups can be defined _a priori_ without reference to the variables measured (Dueser et al., 1976). In the combined microtine analysis the groups are the microtine species. In the analysis of used vs. unused microhabitats the groups are the presence or absence of a species at a given trap station. Therefore, this assumption is upheld. Two additional assumptions, as discussed by Green (1971, 1974), are the assumptions of multivariate normality and equality of the variance-covariance matrices. Tests for the equality of the variance-covariance matrices indicated that the data do not meet this assumption. However, as reported by Klecka (1980), discriminant analysis is very robust to the assumptions of multivariate normality and homogeneity of the covariance matrices and therefore these assumptions need not be strictly adhered to.

Analysis of variance, with a Bonferroni means separation test, was used to document significant differences between species means for the 14 habitat variables included in the discriminant functions. Spearman's rank correlation coefficients were used to assess significant correlations ($\underline{P} < 0.01$) between the number of captures at a trap station and the corresponding habitat variables. Spearman's coefficient was also used to assess correlations between the three vole species. To assess spatial distribution patterns, I calculated the number of trap stations that captured only one of these species compared to trap stations capturing two or all three vole species.

RESULTS

Eutamias townsendii (Townsend's chipmunk) and Peromyscus maniculatus (the deer mouse) were the most numerous small mammals on the study grids in terms of relative abundance (Table 2). C. californicus was the third most numerous species with 533 captures. M. oregoni (306 captures) and M. richardsoni (119 captures) ranked sixth and eighth, respectively, in terms of relative abundances. Other members of the order Rodentia included Zapus trinotatus, (Pacific jumping mouse), Glaucomys sabrinus (northern flying squirrel), and Neotoma cinerea (bushy-tailed woodrat). Insectivores included several shrew species (Sorex spp.), Neurotrichus gibbsii (shrew-mole), and Scapanus orarius (Oregon coast mole). Mustela erminea (short-tailed weasel), and Mustela frenata (long-tailed weasel) represented the family Mustelidae.

C. californicus was captured 2.5 times more frequently in upland than in riparian habitat (Fig. 1). Conversely, M. oregoni was captured 3.5 times more frequently in riparian than in upland habitat. M. richardsoni was caught exclusively in riparian habitat. C. californicus was captured 3.9 more times frequently and M. richardsoni was captured 8.3 times more frequently in old-growth stands (Fig. 2). M. oregoni was captured 1.7 times more often in mature forest stands.

The frequency of *C. californicus* was positively correlated with percent cover of western hemlock and negatively correlated with percent cover of deciduous trees as a group and, specifically, red alder (Table 3). *M. oregoni* was positively correlated with the number of vegetative strata and percent cover of deciduous and evergreen herbs and deciduous shrubs; *M. richardsoni* was positively correlated with plant species richness and deciduous herbs and was negatively correlated with distance from the creek, canopy cover of evergreen trees as a group and, specifically, Douglas-fir. None of the microtine species was significantly correlated with one another at the 0.05 level.

Spatial distribution patterns indicated minimal overlap between the three species (Table 4). No trap stations captured all three species during any of the three years of the study. In 1981, 15% of the stations that captured *C. californicus* also captured *M. oregoni*. For both 1982 and 1983, this value dropped to 9%. No joint captures of *C. californicus* and *M. richardsoni* occurred in 1981 or 1983. In 1982, *M. richardsoni* was captured at 1% of the stations that captured *C. californicus*.

M. oregoni was captured at fewer trap stations than *C. californicus*, therefore stations at which there were joint captures represented a greater percent of the total (18, 22, and 13%, in the three respective years). There were no joint captures of *M. oregoni* and *M. richardsoni* in 1981; in 1982 and

1983 the stations at which both species occurred represented 7% of the total number of stations for _M_. _oregoni_. During years for which joint captures occurred between _M_. _richardsoni_ and either of the two remaining species, these captures represented a greater percent of the total number of stations at which _M_. _richardsoni_ was captured. The overlap with _C_. _californicus_ was 13% in 1982. The overlap with _M_. _oregoni_ was 24% in 1982 and 19% in 1983.

The difference between microhabitats where _C_. _californicus_ was caught vs. those where this species was never caught was highly significant ($P < 0.001$) (Table 5). Six variables were selected by stepwise discriminant analysis as most effectively distinguishing between microhabitats (Table 5). Percent cover of lichen and canopy cover of western hemlock were the most important positively correlated variables distinguishing between microhabitats used by _C_. _californicus_ vs. those available but not used. The canopy cover of deciduous trees was negatively correlated to the discriminant function. Other variables included in the discriminant function were plant species richness, creek distance, and total length of decayed logs (decomposition classes three to five). Using only the six variables in the discriminant function, 70.1% of the cases were correctly classified as to whether or not _C_. _californicus_ was captured at the trap station.

For _M_. _oregoni_, the separation between microhabitat types was also highly significant ($\underline{P} < 0.001$). The three most important variables were the percent cover of evergreen and deciduous herbs and the percent cover of deciduous shrubs (Table 5). These variables were positively correlated with the discriminant function. Leaf litter was a less important variable (i.e., less correlated to the discriminant function). This variable was negatively correlated to the discriminant function. This procedure correctly classified 69.2% of the observations.

For M. richardsoni, the most important positively correlated variable was the percent of exposed soil (Table 5). Highly correlated variables in a negative direction were the canopy cover of Douglas-fir and the 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 ($\underline{P} < 0.001$) (Table 5) and the procedure classified 90.0% of the observations correctly.

Combining the three microtine species in one discriminant procedure identified variables effective in distinguishing between species' microhabitats. This analysis was based on the presence of a given microtine species at a trap station and associated with the corresponding microhabitat variables. This procedure produced two orthogonal and highly significant discriminant functions ($\underline{P} < 0.001$) (Table 6). The most important variables on the first discriminant function were percent cover of lichen, canopy cover of deciduous trees, and the distance to the creek (Table 6). 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 available in the habitat variables. The second function encompassed 18% of the discriminating information and was largely a function of percent cover of evergreen herbs. This analysis correctly classified 73.7% of the observations (Table 7).

Percent cover of deciduous herbs and trees, soil exposure, and total length of recently fallen logs were highest for *M. richardsoni* and lowest for *C. californicus* (Table 7). Conversely, the mean values for lichen, western hemlock, and slope gradient were highest for *C. californicus* and lowest for *M. richardsoni*. Mean value for creek distance was highest for *C. californicus*, averaging 108.0 m. Mean creek distance was 37.7 m for *M. oregoni*, and 3.8 m for *M. richardsoni*. *M. oregoni* had higher values than either *C. californicus* or *M. richardsoni* for percent cover of leaf litter, evergreen herbs, deciduous shrubs, and Douglas-fir.

DISCUSSION

In this assemblage of locally sympatric microtines, microhabitat separation was statistically significant, in spite of overlap in macrohabitat use. *C. californicus* selected microhabitats with a high percent cover of lichen and western hemlock and a low percent cover of deciduous trees. Microhabitats that were selected had a high plant species richness, were located a greater distance from the creek, and contained a greater total length of decayed logs. *M. oregoni* selected microhabitats high in herbaceous vegetation, both deciduous and evergreen, and high in deciduous shrubs. Selected microhabitats were low in leaf litter. *M. richardsoni* selected microhabitats that had a high percent of exposed soil, and Douglas-fir, a greater total length of recently fallen logs, high plant species richness, gentle slope gradient, and decreased percent cover of lichen. Variables most responsible for the significant separation between microhabitats for the three species were lichen, canopy cover of deciduous trees, and distance from the creek.

Clethrionomys californicus is found in moist coniferous forests (Ingles, 1965; Macnab and Dirks, 1941) dominated by red cedar, western hemlock and Douglas-fir (Maser and Storm, 1970). Although the degree of cover varies, the forest cover where this vole occurs is often dense (Bailey, 1936; Macnab and Dirks, 1941).

This species occurs in several seral stages, but is most abundant in old-growth (Maser et al., 1978). In this study, C. californicus was captured 2.5 times more frequently in old-growth than in mature forest stands, and captures were 3.9 times more frequent in upland than in riparian habitats.

Clethrionomys californicus is generally found in close association with logs (Bailey, 1936; Tevis, 1956). Gashwiler (1959) determined that even after logging, enough cull logs and wood debris remained to sustain C. californicus, but this species disappeared within one year after the logs and wood debris were burned. Recently fallen logs apparently provide suitable habitat (Maguire, 1982), but the results of this study and others (Bailey, 1936; Maser et al., 1981) indicate that abundance of C. californicus increases with an increased quantity of highly decayed logs. Protection from predators might be responsible for the association with fallen logs, as suggested by Miller and Getz (1972) for C. gapperi. However, another important factor may be that more highly decayed logs contain high concentrations of mycorrhiza-forming root tips (Maser et al., 1978). C. californicus feeds on hypogeous fungi, particularly of the class Basidiomycetes (Ure and Maser, 1982). This vole detects the fungi primarily by olfaction and uses the fungi as a source of food and perhaps water (Ure and Maser, 1982; Maser et al., 1978). When fungi become scarce in the winter and early spring, lichen (which was significant in the separation of C. californicus from non-*C. californicus* microhabitats) becomes extremely important in the diet (Ure and Maser, 1982). Lichen is also used by this vole for nest building.

Microtus oregoni occupies almost all habitats associated with moist coniferous forests in montane areas (Goertz, 1964; Hooven, 1971). It is most abundant in forest edges and brushland habitats (Goertz, 1964). In British Columbia, Sullivan and Krebs (1981) found that old fields associated with coniferous forest provided optimum habitat. Populations were greater in clearcuts than in undisturbed forests, with clearcuts up to four or five years after logging providing the most suitable habitat (Gashwiler, 1972). After this time period, Gashwiler found no consistent relationship between the age of the clearcut and the abundance of *M. oregoni*. My data indicate that even in undisturbed forests, *M. oregoni* prefers mature over old-growth forests; *M. oregoni* occurred 1.7 times more frequently in mature forests than in old-growth stands. *M. oregoni* was captured 3.5 times more frequently in riparian than in upland habitats.

The association of *M. oregoni* with early successional stages and riparian habitats probably relates to the extensive herbaceous cover in these habitat types (Dyrness, 1965; Gashwiler, 1972). In this study, the deciduous and evergreen components of herbaceous cover were the two most important variables discriminating microhabitats where *M. oregoni* was captured at least once vs. where it was never captured.

Selection of microhabitats high in herbaceous cover probably reflects the diet of M. oregoni. This species has a flexible diet that includes huckleberries and hypogeous fungi, but the main component of the diet is herbaceous vegetation (Maser et al., 1978). In addition to supplying the main dietary component, herbaceous microhabitats may provide protective cover. Based on behavioral observations of captive M. oregoni, Maser et al. (1981) state that these voles seem to prefer protective cover, such as logs and dense vegetation, low enough that their backs are in almost constant contact with it.

Microtus richardsoni is found primarily along montane streamsides (Anderson et al., 1976; Findley, 1951; Murie, 1960; Rassmussen and Chamberlain, 1959; Rust, 1946) and also in marshes, damp meadows, and along upland lakes (Ingles, 1965; Whitaker, 1980). Findley (1951) found M. richardsoni most numerous along open streams, although he also captured these voles in dry, alpine meadows away from water. In my study, M. richardsoni was captured exclusively in riparian habitats.

Although M. richardsoni is generally found at high elevations, various elevations are reported depending on geographical area and vole population densities (Anderson et al., 1976; Racey, 1960). Ingles (1965) states that M. richardsoni is limited to alpine habitats, however other authors are less restrictive. Maser and Storm (1970) report the habitats as primarily alpine and subalpine. Several authors concur, suggesting that this species is found almost exclusively at or immediately below timberline (Anderson et al., 1976; Cowan and Guiget, 1960; Soper, 1967). By contrast, in my study, _M. richardsoni_ was found in dense forests in both mature and old-growth stands. _M. richardsoni_ was captured 8.3 times more frequently in old-growth than in mature forest stands. These results, in terms of macrohabitat selection, contrast with those of Hooven (1971, 1973) who captured _M. richardsoni_ only in logged areas with an open canopy. The microhabitats that _M. richardsoni_ selected in my study did have a low percent cover of Douglas-fir, but had a high percent cover of deciduous trees.

Use of microhabitats adjacent to the stream may be due to the associated microclimate of relatively consistent low temperatures and high humidity (Anderson et al., 1976). _M. richardsoni_ swims readily and may be dependent on water for protection (Bailey, 1936). Recently fallen logs which characterize the microhabitats selected by this species probably provide additional protective cover. Forbs, a primary component of the diet of this vole, are abundant in the microhabitats adjacent to the stream.

Complexity of structure has been suggested to be important in microhabitat selection by desert rodents (M'Closkey, 1976, 1978; Price, 1978; Rosenzweig, 1973; 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 have been found to specialize along the vertical component where the environment is vertically complex (MacArthur, 1958; Rand, 1964). Somewhat surprisingly, several studies of rodent communities have also suggested vertical complexity to be a significant in microhabitat separation (M'Closkey and Fieldwick, 1975; Morris, 1979; Rosenzweig and Winakur, 1969; Stah, 1980). In the current study, the mean foliage height diversity was relatively consistent between the vole species and was not significant in microhabitat separation. Reflecting on the activity patterns of these species (all three species are primarily subterrestrial), it is unlikely that they segregate along the arboreal component to any great extent. In addition, differences of vertical structure may be incorporated adequately in other variables such as percent cover of deciduous shrubs or Douglas-fir.

For both _C_. _californicus_ and _M_. _richardsoni_, plant species richness was important in separating microhabitats used from those available. However, this variable was not important in distinguishing between 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.

The spatial distribution patterns indicated minimal overlap between the speices. There were no trap stations that captured all three voles during any of the three years of the study. Of the trap stations that captured voles, relatively few of these captured more than one species. These distribution patterns may result from competitive interactions between the species. The results of experiments with other vole species indicate that habitat distribution patterns are a result of interspecific competition for space (Grant, 1969, 1970, 1972; Hawes, 1975). Space may be an important resource for vole species in terms of burrowing sites, nesting sites, and refuges from predators. The mechanisms of competition may be visual, olfactory, or auditory cues or physical encounters (DeJonge, 1980; Grant, 1969; Terman, 1974).

Reports of competition between microtine species vary with respect to importance to community structure. Farris (1971) found that habitat distribution of _M. longicandus_ varied independently of manipulated densities of _M. oregoni_, whereas Krebs (1977) found clear evidence of competition between _M. pennsylvanicus_ and _M. ochrogaster_ only in fenced areas of abnormally high densities. Conversely, in a series of experiments in large enclosures, Grant (1970) found shifts in habitat use when either _M. agrestis_ or _M. pennsylvanicus_ were tested with _C. glarelous_ or _C. gapperi_. Grant (1972, 1978) has reviewed these and other experimental studies of competition among rodents. More recently, Schoener (1983) and Connel (1983) have reviewed the experimental evidence for competition among a wide range of taxa including small mammals.

Although I am unaware of experimental investigations into the mechanisms responsible for spatial distribution patterns between the vole species in the current study, Maser et al. (1978) have suggested that it is the dietary specialization of *C. californicus* (primarily hypogeous fungi) and the dietary flexibility of *M. oregoni* (primarily forbs and grasses and secondarily fungi) that allows these two voles to coexist. The fact that *C. californicus* becomes less abundant in younger stands is probably due not only to the direct loss of canopy cover, but also to the cessation of fruiting in the symbiotic fungi when conifers are removed (Ure and Maser, 1982). Conversely, the predominance of *M. oregoni* in younger stands is probably due to the greater herbaceous cover.

The third species, *M. richardsoni*, is a microhabitat specialist, being most abundant adjacent to clear, cool, swift running streams. *M. richardsoni* is one of the largest species in the genus *Microtus*, in contrast to *M. oregoni* which is the smallest (Johnson and Johnson, 1982). Large body size may give *M. richardsoni* a physiological (Smith, 1974) and behavioral advantage (Grant, 1970) and allow it to compete effectively under conditions of low air and water temperatures where elsewhere it may be excluded by more broadly adapted species (Anderson et al., 1976).

Clearly, this study cannot reveal the mechanism by which microhabitat separation is achieved. To determine whether these patterns of spatial distribution are the result of habitat selection (perhaps as an evolutionary adjustment to past competition) or the result of current competition requires experimentation. Resolution lies in the experimental removal or addition of small mammal species or in selective habitat alterations to determine the occurrence and extent of micro- or macrohabitat shift.

In ecological terms, the discriminant analyses suggest that the microhabitat separation between the species is significant and is related to canopy cover of deciduous trees, distance to the creek, and percent cover of lichen. Specifically, *C. californicus* selected microhabitats with a high percent cover of lichen and western hemlock and a low percent cover of deciduous trees. *M. oregoni* selected microhabitats high in deciduous and evergreen herbs and high in deciduous shrubs. *M. richardsoni* was the most specialized species, selecting microhabitats near the creek with a high soil exposure, greater total length of recently fallen logs, and reduced canopy cover of Douglas-fir.

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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 herbs
HERBEV	Percent cover of evergreen herbs
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 to nearest permanent water source (m)
ACMACOV	Canopy cover of big-leaf maple, *Acer macrophyllum*
ALRUCOV	Canopy cover of red alder, *Alnus rubra*

Chapter II

Table 1.--(cont., p.2)

Variable	Description
PSMECOV	Canopy cover of Douglas-fir, *Pseudotsuga menziesii*
TSHECOV	Canopy cover of western hemlock, *Tsuga heterophylla*
P1	Proportion of vegetation in 0.0- 0.25m layer
P2	Proportion of vegetation in 0.25- 0.5m layer
P3	Proportion of vegetation in 0.5- 1.0m layer
P4	Proportion of vegetation in 1.5- 2.0m layer
P5	Proportion of vegetation in 1.5- 2.0m layer
P6	Proportion of vegetation in 2.0- 2.5m layer
FHD	Foliage height diversity, $1/\Sigma pi^2$
SNAGNUM	Number of snags in 100 m^2
AVGLOGDI	Average diameter of logs in $100m^2$

Table 1.--(cont., p.3)

Variable	Description
NEWLOGS	Total length of recently fallen logs, decomposition classes 1 and 2
OLDLOGS	Total length of decayed logs, decomposition classes 3, 4 and 5
SLOPE	Average of upslope and downslope gradient

Table 2.--Number of captures and percent of total captures for undisturbed conditions, 1981 to 1983.

Species	Frequency	Percent
Peromyscus maniculatus	4,984	53.1
Tamias townsendii	2,129	22.7
Clethrionomys californicus	533	5.7
Zapus trinotatus	440	4.7
Sorex trowbridgii	362	3.9
Microtus oregoni	306	3.3
Sorex monticolus	289	3.1
Microtus richardsoni	119	1.3
Glaucomys sabrinus	85	0.9
Scapanus orarius	33	0.4
Neurotrichus gibbsii	42	0.4
Mustela erminea	32	0.3
Neotoma cinerea	15	0.2
Tamiasciuras douglassi	5	0.1
Sorex vagrans	3	0.0
Sorex bendirii	2	0.0
Sorex palustris	2	0.0
Spermophilus beecheyi	1	0.0
Mustela frenata	1	0.0
TOTAL:	9,382	100

Table 3.--Spearman's rank correlation coefficients (*P* <0.01) between microtine species and habitat variables. Plus or minus sign indicates direction of correlation for nonsignificant correlation. **P* <0.01; ***P* <0.001. Variable mnemonics follow those outlined in Table 1.

Variable	*C. californicus* (n = 560)	*M. oregoni* (n = 560)	*M. richardsoni* (n = 560)
STRATNUM	-0.16 **	0.18 **	+
SPECNUM	+	+	0.22 **
SOILEX	-0.16 **	+	+
ROCK	-	+	0.15 **
LEAFLT	-0.11 *	+	-0.11 *
LICHEN	0.22 **	-	-
MOSS	0.12 *	-	-
HERBDC	-	0.31 **	0.20**
HERBEV	-	0.14 **	-
SHRBDC	-	0.16 **	0.17**
SHRBEV	0.25 **	-0.20 **	-0.19 **
TREEDC	-0.36 **	0.11 *	+
TREEEV	0.25 **	-	-0.24 **
CREEKDIS	0.24 **	-0.13 *	-0.34 **
ACMACOV	-0.27 **	0.14 **	+
ALRUCOV	-0.31 **	0.13 *	0.14 **
PSMECOV	+	-	-0.25 **

Chapter II

Table 3.--(cont., p. 2)

Variable	*C. californicus*	*M. oregoni*	*M. richardsoni*
TSHECOV	0.28 **	-	+
P1	+	+	-
P2	+	+	-
P3	+	+	+
P4	-	-	+
P5	-0.12 *	-	-
P6	-0.16 **	-	+
FHD	-0.13 *	-	+
SNAGNUM	0.12 ***	-	-
AVGLOGDI	+	-	-
NEWLOGS	+	-	0.12 *
OLDLOGS	+	-	+
SLOPE	+	-0.12 *	-0.21 **

Table 4.--Number of the trap stations with mixed and single species. No trap stations captured all three species during any of the three years of the study.

	C. californicus	*M. oregoni*	*M. richardsoni*
		1981	
C. californicus	56		
M. oregoni	10	47	
M. richardsoni	0	0	2
		1982	
C. californicus	127		
M. oregoni	13	40	
M. richardsoni	2	4	11
		1983	
C. californicus	59		
M. oregoni	6	37	
M. richardsoni	0	3	13

Table 5.--Summary of stepwise discriminant analysis used to differentiate between microhabitats used vs. those available but not used by the given vole species. Values represent total structure coefficients for habitat variables included in the discriminant functions. The absolute magnitude of the coefficient indicates relative contribution of the habitat variable to the discriminant function; sign indicates direction of contribution ***P* <0.001. Variable mnemonics follow those outlined in Table 1.

Variable or characteristic	*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

Table 5.--(cont., p.2)

Variable or characteristic	*C. californicus*	*M. oregoni*	*M. richardsoni*
OLDLOGS	0.36		
SLOPE			-0.40
Approximate F	21.29**	12.26**	14.40**
Percent correctly classified	70.1	69.2	90.9

Table 6.--Summary of stepwise discriminant analysis used to differentiate between microhabitats used by the three vole species. Total structure coefficients for habitat variables included in the discriminant function for the combined microtine species analysis. Absolute value of the coefficient indicates relative contribution of the habitat variable to the discriminant function; sign indicates direction of contribution. **P <0.001. Variable mnemonics follow those outlined in Table 1.

Variable or	Microtines	
characteristic	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

Table 7.--Estimates of the mean (*X*) and standard error (*S.E.*) for microtine species on the 14 habitat variables included in the discriminant functions. Analysis of variance was used to document significant differences between species means. In each row, means followed by the same letter are not significantly different (Bonferroni means separation test *P* <0.05, using three comparisons). Variable mnemonics follow those outlined in Table 1.

	C. californicus		*M.oregoni*		*M. richardsoni*	
	(n=127)		(n=41)		(n=11)	
Variable	*X*	*S.E.*	*X*	*S.E.*	*X*	*S.E.*
SPECNUM	9.6a	0.39	8.9a	0.70	10.9a	1.35
SOILEX	2.3a	0.67	4.2a	1.19	13.0b	2.29
LEAFLT	16.0a	1.86	18.7a	3.28	14.4a	6.33
LICHEN	2.3a	0.12	1.36	0.21	0.6b	0.40
HERBDC	20.3a	2.06	41.3b	3.62	39.1b	7.00
HERBEV	16.0a	0.01	35.1b	3.49	7.7c	6.72
SHRBDC	36.3a	3.07	53.7b	5.40	48.6ac	10.42
TREEDC	11.4a	2.49	45.66	4.38	72.0b	8.46
CREEKDIS	108.0a	6.32	37.7b	11.12	3.8b	21.47

Chapter II

Table 7.--(cont., p. 2)

	C. californicus		M. oregoni		M. richardsoni	
	X	S.E.	X	S.E.	X	S.E.
PSMECOV	37.1a	3.06	42.0a	5.38	0.0b	10.39
TSHECOV	39.7a	3.10	10.7b	5.46	10.5b	10.53
NEWLOGS	8.0a	1.31	8.9a	5.29	11.7a	4.44
OLDLOGS	28.6a	1.75	20.5b	3.07	13.6b	5.94
SLOPE	39.6a	2.03	33.3ab	3.57	16.1b	6.89

Fig.2.1.--Frequency of captures of microtines in riparian vs. upland habitats. Trap effort was equivalent between riparian and upland habitats.

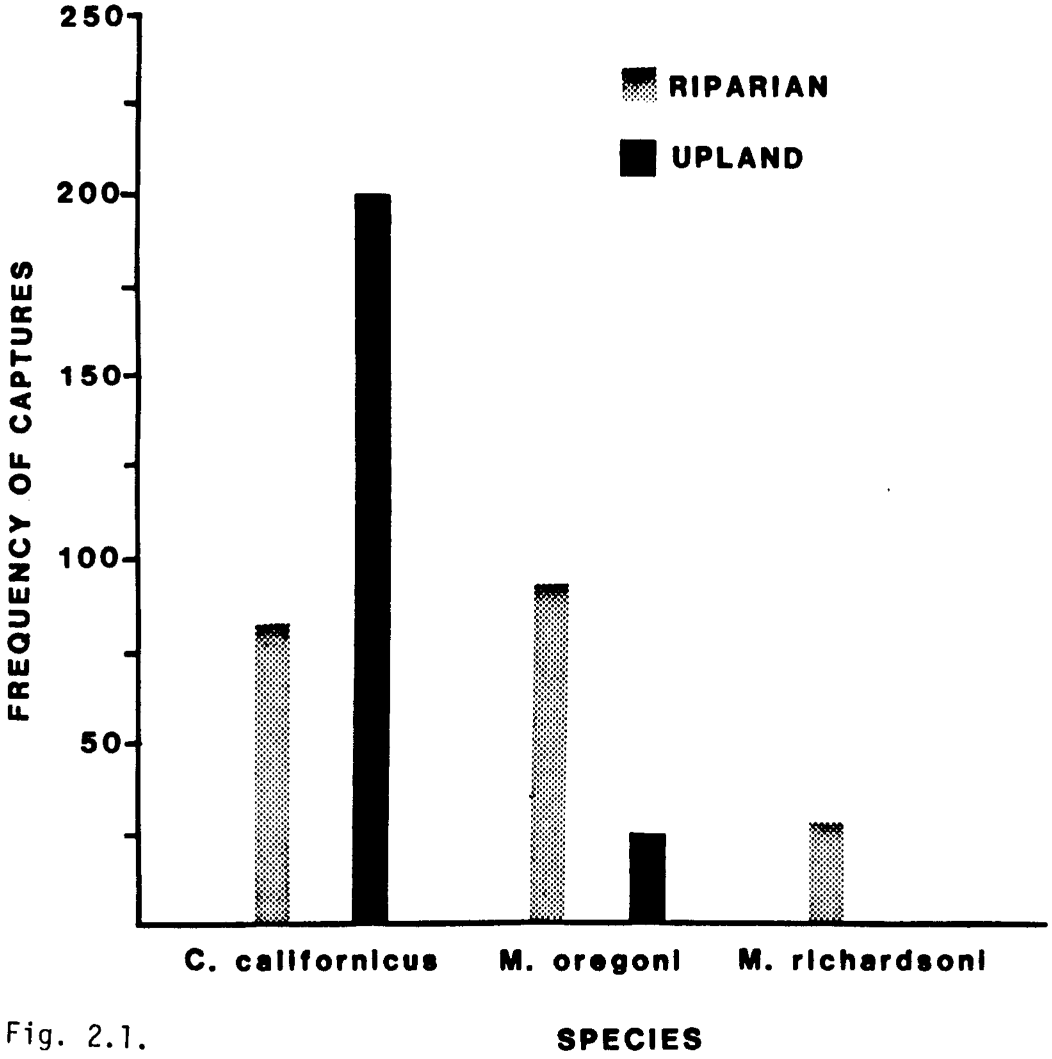
250
200
150
100
50
FREQUENCY OF CAPTURES
▨ RIPARIAN
■ UPLAND
C. californicus
M. oregoni
M. richardsoni
SPECIES

Fig. 2.1.

Fig.2.2.--Frequency of captures of microtines in old-growth vs. mature forest stands. Trap effort was equivalent between riparian and upland habitats.

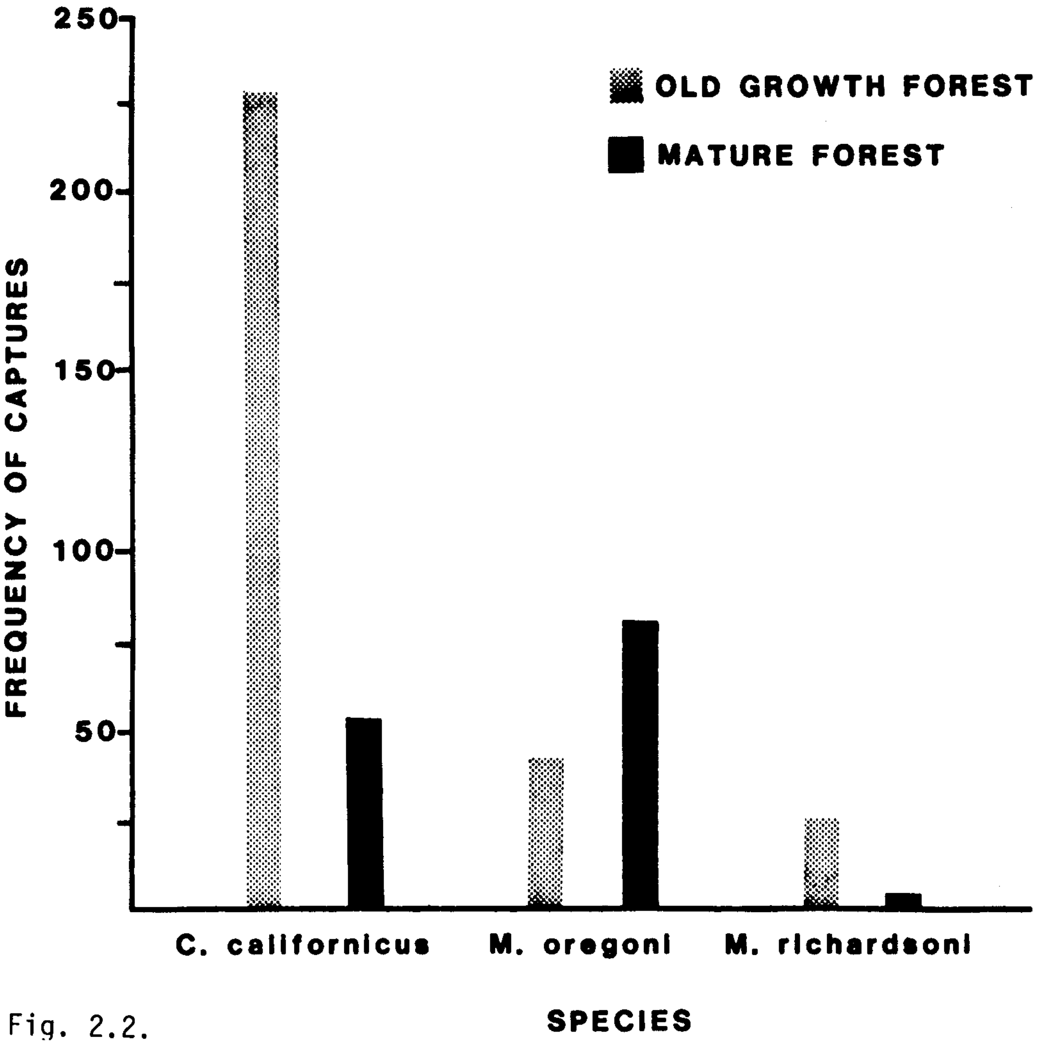
250
200
150
100
50
FREQUENCY OF CAPTURES
▩ OLD GROWTH FOREST
■ MATURE FOREST
C. californicus
M. oregoni
M. richardsoni
SPECIES

Fig. 2.2.

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CHAPTER III

COMPETITION IN A SMALL MAMMAL COMMUNITY: EFFECTS OF A REMOVAL

ABSTRACT

Mark-recapture was conducted during the summer and fall seasons of 1981 through 1983 in the western Cascade Range of Oregon. During 1983, Peromyscus maniculatus, the most abundant small mammal species, was removed from four experimental grids. This was done to investigate patterns of potential competition with remaining species. Previous trapping on experimental grids provided temporal controls. Each experimental grid also had a paired control similar in stand age, habitat, and trap effort. Twenty species were represented in the study for a total of 11,696 captures.

All species of the order Insectivora increased relative to most parameters measured with the removal of P. maniculatus. These parameters included numbers of captures and individuals, numbers of stations utilized per individual, and activity levels. Numbers of captures were significantly higher on the removal grids for Sorex monticolus, Sorex bendirii, Sorex trowbridgii and Scapanus orarius. In the order Rodentia, Zapus trinotatus and

Glaucomys sabrinus both increased with the removal of *P. maniculatus*, suggesting responses to release from competition with *P. maniculatus*. Conversely, *Tamias townsendii* had significantly lower numbers of captures and individuals on experimental grids. The removal of *P. maniculatus* left *T. townsendii* as the most abundant small mammal species on experimental grids. It is possible that predators "switched" to *T. townsendii* thereby effectively depressing densities of *T. townsendii* on the removal grids.

INTRODUCTION

The distribution of species in an area is determined by differential survival and reproduction, habitat selection, predation, dispersal abilities, and intra- and interspecific competition. Many observational studies have suggested that interspecific competition plays an important role in small mammal community structure. However, only recently have controlled experimental field studies been conducted on small mammals (e.g., Abramsky et al., 1979; Abramsky and Sellah, 1982; Blaustein, 1980; Chappell, 1978; Holbrook, 1979; Koplin and Hoffman, 1968; Price, 1978; Redfield et al., 1977; Schroder and Rosenzweig, 1975). Experiments (through species removals, additions, or both) are required to provide evidence for competition (Connell, 1975). If a species that is removed is competitive with the remaining species then population expansion, or distribution expansion, of the remaining species should occur. Grant (1972; 1978) reviewed some of the experimental studies of competition between small mammal species. Controlled experiments on unconfined populations are the most likely to answer questions about the importance of interspecific competition in natural communities.

The present study examined the role of interspecific competition between the most abundant small mammal species, _Peromyscus maniculatus_, and the remaining small mammal species.

P. maniculatus were removed from four of eight unenclosed trapping grids during the third year of the study. Changes in relative abundance, activity levels, and number of trap stations used per individual were used to assess the role of competition for space or food between the species.

METHODS

Study area

Field research was conducted in the western Cascade Range in near Blue River, Oregon, approximately 75 km east of Eugene, Oregon. This area is characterized by well-defined drainages and steep slopes. Soil is primarily a clay loam, volcanic in origin (Gashwiler, 1972). Bedrock is comprised of the Oligocene-Miocene Western Cascade Group (Franklin and Dyrness, 1971).

Annual precipitation ranges from 2,300 mm to 2,800 mm, 90% of which falls between October and April (Franklin and Dryness, 1971). Above 900 m, snowpacks accumulate to 1 m or more. Temperatures are moderate with a mean July maximum of 29^{o}C and mean January minimum of -3^{o}C. A more complete description of the soils, climate, and bedrock can be found in Franklin and Dyrness (1971).

Four study sites were selected: two along Lookout Creek, a fourth order (Strahler, 1957) stream on the H. J. Andrews Experimental Forest; one along Hagan Creek, a fourth order stream in the Hagan Research Natural Area; and one along Marten Creek, a fifth order stream in the Eugene District of the Bureau of Land Management. The Upper and Lower Lookout sites are old-growth stands, approximately 250 years old. Hagan and Marten are mature forest stands, approximately 100 years old. Study sites were separated from one another by a distance of at least 2.8 km.

Douglas-Fir (*Pseudotsuga menziesii*) represents the most abundant conifer on the study sites. Other conifers include western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), silver fir (*Abies amabilis*), grand fir (*Abies grandis*), and Pacific yew (*Taxus brevifolia*). The primary deciduous trees are big-leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and vine maple (*Acer circinatum*). The predominant ground cover includes salal (*Gaultheria shallon*), western swordfern (*Polystichum munitum*), Oregon grape (*Berberis nervosa*), and Oregon oxalis (*Oxalis oregona*).

Trapping procedure

At each of the four sites, two trapping grids were established, one in riparian habitat and one in nearby upland habitat. The riparian and upland grids at a given site were separated from one another by approximately 150 m, depending on the width of the transition zone. All grids were unenclosed. In 1981, each grid consisted of 56 trap stations. During 1982 and 1983 each grid was expanded to 70 trap stations. All grids had a grid interval of 10 m. Because of the linearity of the riparian habitat, the Upper Lookout riparian grid consisted of 2 x 35 stations. All other grids were 7 x 10. One large Sherman live trap (8 x 9 x 23 cm) was placed at each trap station within 1 m of the grid coordinate and was baited with a mixture of whole oats and sunflower seeds. Unbaited, unset traps were positioned at the trap stations for at least one week prior to trapping to minimize a neophobic reaction to the traps. Traps were set lightly to effectively sample juveniles as well as adults.

Traps were checked each morning as soon as light was sufficient to process the mammals. Species, sex, age class, weight, and reproductive condition were noted. Age classes were determined by body weights. For each species, the minimum weight at which individuals were reproductively active was determined. Animals equal to or over this weight were classified as adults. For species for which there were fewer than 15 captures of reproductively active individuals of a given sex, I used the minimum cutpoints (Maser et al., 1981; Burt and Grossenheider, 1976) to classify animals as juveniles vs. adults. Each animal was marked by toe clipping prior to release at the capture site. All scientific and common names follow Jones et al. (1982).

Trapping was conducted during the months of July through November of 1981 and June through November of 1982 and 1983, for a trap effort of 52,752 trap nights. In 1983, four of the eight grids had _P. maniculatus_ removed for a trap effort of 12,600 trap nights. Trapping on the experimental grids in 1981 and 1982 provided temporal controls. In addition, each experimental grid had a paired control similar in stand age, habitat, and trap effort. Table 1 outlines the trapping grids and the corresponding stand age, habitat, and experimental treatment. On the experimental grids, all individuals of *P. maniculatus* were removed via intensive live trapping throughout the field season. Intensive live trapping was also conducted on the control grids throughout the field season, however, *P. maniculatus* were not removed from the control grids.

Data analysis

Species composition was assessed using number of captures and number of individuals and was analyzed using chi-square tests. The mean number of captures of a given species per utilized trap station was calculated as a measure of species activity. This was calculated as the number of captures of a species divided by the number of stations at which the captures occurred. T tests were used to determine if there were significant differences in the mean number of captures per trap station utilized on experimental vs. control grids.

Mean number of captures per individual was used to indicate the amount of activity per individual on control vs. experimental grids. The mean number of trap stations used per individual indicated the relative expansion or restriction in microhabitat use between control and experimental grids. Statistical significance of the difference between treatments was assessed via t tests for each of these variables. Significance levels for t tests were assessed with a Bonferroni means separation test.

Presentation and interpretation of trapping data will focus on results of species removals conducted in 1983. Premanipulation patterns, i.e, results of trapping data from 1981 and 1982, will be used to clarify results of experimental removals.

RESULTS

There were 11,696 captures of 20 small mammal species on the study sites from 1981 through 1983. Seven species of Insectivora were captured (9.2% of the total captures). The most abundant insectivore species were *Sorex trowbridgii* and *S. monticolus*. Eleven species of rodents were captured (90.4% of the total captures). *P. maniculatus* and *Tamias townsendii* were the most abundant rodent species. *Mustela erminea* (39 captures) and *M. frenata* (five captures) represented 0.3% of the total captures.

Distributional data

In 1983, 534 *P. maniculatus* were removed from the experimental grids (Table 2). The number of individuals removed was significantly higher than the number of individuals captured on the control grids. All plots were unfenced and therefore the individuals removed probably included both residents and immigrating animals. Although it is desirable to completely remove the species of concern to document the effects of competition, this is impossible on unenclosed plots. Intensive trapping and removal of *P. maniculatus* did result in a highly significant decrease in the number of captures of *P. maniculatus* on removal vs. control grids (Table 3). The number of captures of *P. maniculatus* on removal grids represented only 15% of the total number of captures for this species in 1983.

Although not all values were statistically significant, in the order Insectivora all species that were captured in 1983 were represented by a higher number of captures and number of individuals captured on the removal than on the control grids (Tables 2 and 3). For Sorex monticolus, S. bendirii, and S. trowbridgii both number of captures and number of individuals were significantly higher on removal than control grids. For Scapanus orarius, the number of captures was significantly higher on the removal grids. Neither Sorex vagrans nor S. palustris were captured in 1983.

For both Scapanus orarius in 1981 and Sorex monticolus in 1982, the numbers of captures and the numbers of individuals were significantly higher on the control grids. It was only for Sorex trowbridgii in 1981 that these variables were significantly higher on the pre-manipulation "removal grids" than on the control grids. This indicates that the increases in numbers of captures and numbers of individuals on removal grids on removal grids in 1983 were most likely not artifacts of higher pre-manipulation densities on removal grids.

In the order Rodentia, only G. sabrinus had both a significantly higher number of captures and number of individuals on the removal grids in 1983 (Tables 2 and 3). Z. trinotatus had a significantly higher number of captures on the removal grids, but the number of individuals was not significantly different. Conversely, T. townsendii had significantly more captures and individuals on the control grids. Two microtine species, *C. californicus* and *Microtus richardsoni*, also had significantly higher values on the control grids. *C. californicus* had a higher number of individuals and *M. richardsoni* had a higher number of captures.

In previous years, neither number of captures nor individuals for *G. sabrinus* was significantly different between removal and control grids. *Z. trinotatus* had significantly higher captures on the control grids in 1981 and on removal grids in 1982. *T. townsendii* had significantly higher captures on removal grids in 1981 and a higher number of individuals on the control grids in 1982. *C. californicus* had a significantly higher number of captures and individuals on control grids in 1982. Number of captures and number of individuals were also higher for *Microtus oregoni* on control grids for both 1981 and 1982. These trapping results from pre-manipulation field seasons indicate that for most of the rodent species, the experimental results may accurately reflect responses to removal of *P. maniculatus*. However, for both *C. californicus* and *Microtus oregoni*, the numbers of captures and individuals on control in 1983 may reflect pre-manipulation densities rather than a response to the removal of *P. maniculatus*.

In the order Carnivora, *Mustela erminea* had a higher number of captures and individuals on the control grids.
Pre-manipulation values in 1982 were also significantly higher on

the control grids. Although the sample size was small, the number of captures and individuals of _M. frenata_ was significantly higher on the removal grids in 1983.

Activity patterns

The mean number of captures per trap station utilized indicated the intensity of activity on the portions of the grid a given species used. Although low recapture rates make this a difficult parameter to evaluate in Insectivora (see Hawes, 1977), _S. trowbridgii_ had significantly higher activity levels on removal grids than on control grids in 1983 (Table 4). Pre-manipulation years showed no significant differences between control and removal grids for any species in the order Insectivora.

Zapus trinotatus was the only rodent species that had a significantly higher activity level on removal grids in 1983 (this variable was not significantly different in previous years). _P. maniculatus_ was the only rodent species for which activity level was significantly higher on the control grids in 1983. In 1982, activity levels were also significantly higher on the control grids. Activity levels were not significantly different in 1983 for _C. californicus_. However, as with numbers of captures and individuals, the 1983 activity level may not accurately reflect a response (or lack of response) to removal of _P. maniculatus_ since the 1982 activity levels were significantly higher on control grids. Activity level was not significantly different between treatments for the order Carnivora.

The number of captures per individual was also used as a measure of activity. As expected, for *P. maniculatus* the activity per individual was significantly higher on the control grids in 1983 (Table 5). Both *Sorex monticolus* and *Z. trinotatus* had significantly higher activity levels per individual on the removal grids. Neither of these species had significantly different activity per individual between treatments during previous years.

Mean number of stations per individual indicated the relative expansion or restriction in distribution between removal and control grids. There were no species in the order Insectivora for which significant differences between removal and control grids were found during any of the three years (Table 6). For *P. maniculatus*, the number of stations used per individual was, as expected, significantly higher on the control grids. Conversely, *Z. trinotatus* had a significantly higher number of stations per individual on removal grids in 1983. Significant differences did not occur in previous years. No significant differences were found in the order Carnivora.

Mean adult weight

Mean adult weight may indicate habitat quality (Van Horne, 1982). In addition, particularly in a species removal study, mean adult weight may indicate size and, by inference, social status of immigrating individuals. The mean adult weight of *Sorex monticolus* was significantly lower on the removal grids in 1983 (Table 7). These values were not significantly different in previous years.

Despite the fact that for both pre-manipulation years the adult weight of *P. maniculatus* was significantly higher on the removal grids, adult weight was significantly lower on removal grids in 1983. For *T. townsendii* and *G. sabrinus*, adult weight was significantly lower on removal grids in 1983. Although adult weight was not significantly different in previous years for *G. sabrinus*, adult weight of *T. townsendii* was significantly lower on removal grids in 1982 as well as 1983. This indicates that for *T. townsendii* significant differences detected in 1983 may not reflect a response to removal of *P. maniculatus*, but instead may indicate subtle differences in habitat quality, differences in age structure, or other alternative factors.

Only one rodent, *C. californicus*, had significantly higher adult weights on the removal grids in 1983. Although mean adult weight of *C. californicus* was not significantly different in 1982, it was significantly higher on the removal grids in 1981. Significant differences were not detected for *Mustela erminea* during any of the three years.

DISCUSSION

All species of the order Insectivora increased relative to most parameters measured with the removal of *P. maniculatus*. Numbers of captures were significantly higher on the removal grids for *Sorex monticolus*, *S. trowbridgii*, and *Scapanus orarius*. Although this study cannot determine the specific mechanism responsible for the increased abundance of several small mammal species, the response may be as a result of release from exploitative competition for food. Exploitative competition, as defined by Colwell and Fuentes (1975) is mediated by a resource which is sufficiently lowered by one species that another species is excluded from a portion of the niche common to the fundamental niches of the two species. It is therefore based on differential efficiency of resource utilization. High recruitment rates, such as those found in *P. maniculatus* (King, 1968), may influence the differential ability to utilize resources (Schoener, 1983). Schoener found that exploitative competition and interference competition (competition requiring a more direct interaction) were represented about equally as apparent mechanisms of competition. *P. maniculatus* is an omnivorous species and feeds on a wide variety of invertebrates, seeds, fruits, and hypogeous fungi (Burt and Grossenheider, 1976; Maser et al., 1981; Whitaker, 1980). Although Gunther et al. (1983) found the primary food of *P. maniculatus* in clearcuts to be conifer seeds, in forests the primary food is invertebrates (Gunther et al., 1983). Food that is not consumed immediately is cached in hollow logs, or other protected areas, for future use (Whitaker, 1980).

The shrew species in this study feed primarily on a wide variety of invertebrates including adult and larval insects, spiders, terrestrial snails, earthworms, and centipedes (Jameson, 1955; Gunther et al., 1983; Whitaker, 1980; Whitaker and Maser, 1976). In addition, these species feed to some extent on conifer seeds, hypogeous fungi, and lichens (Gunther et al., 1983; Whitaker and Maser, 1976). The two mole species, Neurotrichus gibbsii and Scapanus orarius, also have a diet composed primarily of invertebrates and secondarily of seeds and lichens (Gunther et al., 1983; Maser et al., 1981; Whitaker et al., 1979). There is therefore likely to be an extensive overlap in food resource utilization between P. maniculatus and members of the order Insectivora.

Due to the aggressive behavior patterns in species in the order Insectivora it seems unlikely that P. maniculatus could outcompete, in terms of interference competition, even the smaller members of this order. However, the abundance of P. maniculatus on the study sites in undisturbed conditions may result in a decreased availability of terrestrial invertebrates and hypogeous fungi.

Two members of the order Rodentia, G. sabrinus and Z. trinotatus, increased with removal of P. maniculatus. G.

sabrinus, which increased both in captures and individuals, feeds almost exclusively on hypogeous fungi during the summer and autumn seasons (Gunther et al., 1983; Maser et al., 1978; McKeever, 1960). In winter the main food source is lichen (Ingles, 1965; McKeever, 1960). This squirrel also consumes smaller quantities of green vegetation, insects, seeds, and fruits (Maser et al., 1981).

Z. trinotatus increased in number of captures, activity levels, and number of stations utilized per individual on the removal grids. This species feeds on seeds, especially grass seeds, and fruits such as Rubus and Vaccinium (i.e., thimbleberry, salmonberry, evergreen huckleberry, etc.) (Jones et al., 1978; Maser et al., 1981). Subterranean fungi, is also an important component of the diet (Jones et al., 1978). The chief animal food is lepidopterous larvae (Jones et al., 1978). Most fruits are consumed by Z. trinotatus after they ripen and fall to the ground (Maser et al., 1981). Because P. maniculatus is more highly arboreal, this species may be able to obtain seed and fruit food sources before they become available to Z. trinotatus. In addition, the high recruitment abilities of P. maniculatus (King, 1968) may enable this species to outcompete other species for food or other resources.

Unlike the above species, for T. townsendii the number of captures and individuals were significantly higher on control grids in 1983. Although the relative abundance of T. townsendii in undisturbed conditions was highly correlated with P. maniculatus (P<0.001), it is unlikely that a symbiotic relationship between these species is responsible for the significantly lower values on the removal grids. Removal of P. maniculatus left T. townsendii as the most abundant rodent species on the experimental grids. It is possible that predators "switched" (Krebs, 1978) to T. townsendii and therefore depressed densities of T. townsendii on the removal grids more effectively than on the control grids in the presence of P. maniculatus. The predators in the study area include short-tailed weasel (Mustela erminea), long-tailed weasel (Mustela frenata), coyote (Canis latrans), bobcat (Felis rufus), black bear (Ursus americanus), and spotted skunk (Spilogale gracilis). However, since these predators have large home range sizes (Burt and Grossenheider, 1976), it is possible that these species search alternate sites rather than switch prey items.

For C. californicus and Microtus oregoni the numbers of captures and individuals were significantly higher on control grids than on experimental grids in 1982, prior to the removal of P. maniculatus. The numbers of captures and individuals in 1983 probably reflects pre-manipulation densities rather than a response (or lack of response) to the removal of P. maniculatus.

Mustela erminea had lower values on the removal grids in 1983 for all parameters measured except mean adult weight. M. erminea preys primarily on small mammals such as P. maniculatus, *T. townsendii*, *C. californicus*, *Microtus* sp., *Z. trinotatus*, *Sorex* sp., and *Neurotrichus gibbsii* (Maser et al., 1981). Lower values on the removal grids may result from the decreased abundance of *P. maniculatus*, an important prey species and previously the most abundant small mammal. Alternatively, lower values for these parameters may reflect pre-manipulation differences between control and removal grids; numbers of captures and individuals were also significantly lower on the removal grids in 1982.

Mean adult weight was significantly lower on removal grids for *P. maniculatus* in 1983, indicating that immigrating individuals were of lower weight and were probably subdominants. Most species in the orders Insectivora and Rodentia also had lower mean adult weights on removal grids. *C. californicus* was the one rodent with significantly higher adult weight on removal grids.

Interspecific competition occurs when organisms of different species use common, limited resources or when these organisms harm each other in the process of obtaining resources, whether or not resources are limited (Birch, 1957). This process and its relative importance in structuring community organization has been a focal point in ecology. Laboratory research by Gause (1932) demonstrated the inability of two species of yeast to coexist when grown in mixed cultures. The resulting hypothesis, which was never formally defined by Gause, is called the competitive exclusion principle. This principle states that two or more species cannot occupy the same niche because one species will be more successful and eventually occupy the niche exclusively (Hardin, 1960). Hutchinson (1958) further refined our concepts of competition by redefining a species niche as an n-dimensional hypervolume comprised of the total array of variables describing the place of the species in the environment. Field evidence for interspecific competition has been reviewed by Colwell and Fuentes (1975), Connell (1983) and Schoener (1983). Both Connell and Schoener found interspecific competition to be pervasive in ecological systems. However, Connell assessed that of the few studies where inter- and intraspecific competition was separated, intraspecific competition was as strong or stronger than interspecific competition in three-quarters of the experiments. Classically, competition has been defined as negatively affecting all species involved. However, Schoener (1983) found that asymmetry in the effect of competition is common. Schoener suggested that reasons for this asymmetry include differences in 1) the degree to which their resources overlap, 2) size, 3) feeding parameters, 4) recruitment abilities, and 5) responses to harsh environmental conditions.

Interspecific competition is difficult to evaluate; behavioral interactions among many species, particularly small mammal species, are not readily observed in the field. Competitive effects on rare species may be especially difficult to measure (Schoener, 1983). However, laboratory studies may simplify and alter the species environment to the extent that behavioral responses are not applicable. Despite technical problems of removal studies, these studies provide the most direct evidence of interspecific competition (Chappell, 1978).

Inability to detect competition may not mean that competition has never been important in structuring the community organization. Instead, competitive interactions between species may have resulted in one or both species occupying somewhat different habitats. This differential habitat selection could become genetically based and could minimize or eliminate current competition. Coexistence could occur if each species had a refuge in which it was a superior competitor (Hutchinson, 1958). Under these conditions, we would observe competition only when species removals, or additions, are maintained for time periods long enough to allow habitat preferences to be altered by natural selection (Schroder and Rosenzweig, 1975). Connell (1980) outlines the evidence that would be required to demonstrate coevolutionary divergence of competitors, or "the ghost of competition past."

Wiens (1977) has suggested that although competition may play an important role in determining resource utilization patterns, competition probably occurs sporadically, during periods of resource limitation. Therefore we should not always expect to find evidence of competition, particularly during short-term studies. Small mammal studies for which evidence has not been supported the hypothesis that interspecific competition caused shifts in resource utilization include studies by Abramsky and Sellah (1982), Cameron (1977), Krebs (1977), and Schroder and Rosenzweig (1975).

Although I am unaware of any P. maniculatus removal studies testing for competition with the species found in my study area, some experimental studies have been done with congeneric species. Cranford (1978) reported that, in an alpine environment, after Z. princeps emerged from hibernation in the spring, the densities of P. maniculatus decreased. Conversely, P. maniculatus increased after Z. princeps went into hibernation in the fall. When Z. princeps was removed from one of the grids, the spring decrease in density of P. maniculatus did not occur. Lab studies indicated that after 24 hours Z. princeps was behaviorally dominant over and restricted movements of P. maniculatus. Field observational data indicate that Z. hudsonius may be competitively dominant over P. leucopus (Nichols and Conley, 1981).

In terms of interactions with microtine species, Crowell (1976) reported that C. gapperi displaced both P. maniculatus and Microtus pennsylvanicus from wooded habitats and that P. maniculatus displaced M. pennsylvanicus from shrubby habitats. Grant (1970) tested P. maniculatus in enclosures with both C. gapperi and M. pennsylvanicus. M. pennsylvanicus used the grassland portion of the enclosure more frequently when tested with *P. maniculatus* than under control conditions. *P. maniculatus* used the woodland portion more frequently when tested with mainland *M. pennsylvanicus* but not with island members of this species. There were no significant differences in vegetation use when *P. maniculatus* and *C. gapperi* were tested together.

Rowley and Christian (1976) found that in interspecific encounters in a neutral arena female *P. leucopus* were dominant over female *M. pennsylvanicus* in similar breeding conditions. Although their mates did not attack, lactating *P. leucopus* were observed to attack juvenile *M. pennsylvanicus* (Rowley and Christian, 1977). One juvenile that survived chronic exposure to *P. leucopus* did not attain sexual maturity.

It is very difficult to discern the specific mechanisms of competition or even the general classes of mechanisms, e.g., consumptive or encounter competition (Schoener, 1983), in field studies. Laboratory studies such as those by Blaustein (1980), Cameron (1971), De Jonge (1980), King (1957), and Rowley and Christian (1976, 1977) indicate the importance of aggression in interactions between small mammal species. Visual, olfactory, and auditory cues of potential competitors and encounters with potential competitors may result in shifts in resource utilization (Cameron, 1971; De Jonge, 1980; Grant, 1969). However, as Schoener (1983) and Roughgarden (1983) reported, the importance of interference competition may be distorted because it is more observable than exploitative competition.

There are alternative explanations that may account for the responses observed in this study. It is possible that by removing the most abundant small mammal species other small mammal species increased due to altered predator - prey interactions. Alternatively, it is possible that removal of P. maniculatus caused an apparent increase in abundances and activity levels of several small mammal species due to increased trap availability. To test whether the increases in the abundances of several species in the current study are a response to release from exploitative competition would require artificial supplementation of the resources in question (Schoener, 1983). Exploitative competition could be for food resources or could be for space such as burrowing sites, nest sites, breeding sites, or refuges from predators. Although not possible to discern from the current study, it seems likely that food resources, for which there is an extensive overlap in utilization, are an important limiting factor. Supplementation of larval insects, particularly lepidopterous larvae because of its importance in the diet for P. maniculatus, would help elucidate the mechanisms responsible for the increase in several small mammal species.

In summary, all species of the order Insectivora increased relative to most parameters measured with the removal of P. maniculatus. These parameters included the numbers of captures and individuals, numbers of stations utilized per individual, and activity levels. In the order Rodentia, _Zapus_ _trinotatus_ and _Glaucomys_ _sabrinus_ both increased with the removal of _P_. _maniculatus_. Increase of the small mammal species may be responses to release from exploitative competition with _P_. _maniculatus_. Conversely, _Tamias_ _townsendii_ had significantly lower numbers of captures and individuals on the experimental grids. The removal of _P_. _maniculatus_ left _T_. _townsendii_ as the most abundant species on the experimental grids. It is possible that predators "switched" to _T_. _townsendii_ thereby depressing densities of this species on the removal grids.

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Chapter III

Table 1.--Trapping grids and experimental treatments. Removal of *P. maniculatus* was conducted in 1983 for a total of 3,150 trap nights per experimental grid.

Site	Stand age	Habitat	When trapped	Trap nights	Species treatment
Hagan	Mature	Riparian	1981-1983	6,902	*P. maniculatus* removed
		Upland	1981-1983	6,902	*P. maniculatus* removed
Marten	Mature	Riparian	1981-1983	6,902	Control
		Upland	1981-1983	6,902	Control
Lower Lookout	Old-growth	Riparian	1981-1983	6,902	*P. maniculatus* removed
		Upland	1981-1983	6,902	*P. maniculatus* removed
Upper Lookout	Old-growth	Riparian	1982-1983	5,670	Control
		Upland	1982-1983	5,670	Control

Table 2.--Number of individuals (and percent) on removal vs. control grids. Chi-square tests were used to document significant differences between removal and control grids. For 1982 and 1983, trap effort was equivalent between the removal and control grids. Because Upper Lookout was not trapped in 1981, the expected values for removal grids were twice those for control grids during this year. *P<0.05; **P<0.01; ***P<0.001.

	1981		1982		1983	
Species	Removal	Control	Removal	Control	Removal	Control
Order Insectivora						
Sorex vagrans	3(100.0)	0(0.0)				
Sorex monticolus	33(57.9)	24(42.1)	41(37.6)	68(62.4) **	99(59.3)	68(40.7) *
Sorex palustris			0(0.0)	2(100.0)		
Sorex bendirii			0(0.0)	2(100.0)	11(100.0)	0(0.0) ***
Sorex trowbridgii	71(79.8)	18(20.2) **	85(50.6)	83(49.4)	184(71.0)	75(29.0) ***
Neurotrichus gibbsii	14(66.7)	7(33.3)	11(68.8)	5(31.2)	9(69.2)	4(30.8)
Scapanus orarius	1(12.5)	7(87.5) **	4(36.4)	7(63.6)	8(72.7)	3(27.3)
Order Rodentia						
Tamias townsendii	53(72.6)	20(27.4)	65(40.4)	96(59.6) *	106(41.4)	150(58.6) **
Spermophilus beecheyi					0(0.0)	1(100.0)
Tamiasciurus douglasii	1(50.0)	1(50.0)	0(0.0)	1(100.0)	2(66.7)	1(33.3)
Glaucomys sabrinus	12(80.0)	3(20.0)	7(41.2)	10(58.8)	37(63.8)	21(36.2) *

Table 2.--(cont., p. 2)

Species	1981 Removal	1981 Control	1982 Removal	1982 Control	1983 Removal	1983 Control
Order Rodentia (cont.)						
Peromyscus maniculatus	179(66.8)	89(33.2)	45(36.3)	79(63.7) **	534(56.1)	418(43.9) ***
Neotoma cinerea	4(100.0)	0(0.0)	4(100.0)	0(0.0) *	2(100.0)	0(0.0)
Clethrionomys californicus	26(68.4)	12(31.6)	16(17.6)	75(82.4) ***	12(27.9)	31(72.1) **
Arborimus albipes					1(100.0)	0(0.0)
Microtus oregoni	19(42.2)	26(57.8) ***	14(29.8)	33(70.2) **	18(38.3)	29(61.7)
Microtus richardsoni	1(100.0)	0(0.0)	9(90.0)	1(10.0) *	10(55.6)	8(44.4)
Zapus trinotatus	8(53.3)	7(46.7)	74(53.2)	65(46.8)	57(49.1)	59(50.9)
Order Carnivora						
Mustela erminea	2(50.0)	2(50.0)	0(0.0)	7(100.0) **	7(29.2)	17(70.8) *
Mustela frenata	1(100.0)	0(0.0)			4(100.0)	0(0.0) *

Table 3.--Number of captures (and percent) on removal vs. control grids. Chi-square tests were used to document significant differences between removal and control grids. For 1982 and 1983, trap effort was equivalent between the removal and control grids. Because Upper Lookout was not trapped in 1981, the expected values for removal grids were twice those for control grids during this year. *$P<0.05$; **$P<0.01$; ***$P<0.001$.

	1981		1982		1983	
Species	Removal	Control	Removal	Control	Removal	Control
Order Insectivora						
Sorex vagrans	3(100.0)	0(0.0)				
Sorex monticolus	36(55.4)	29(44.6)	54(36.0)	96(64.0) ***	118(62.4)	71(37.6) ***
Sorex palustris			0(0.0)	2(100.0)		
Sorex bendirii			0(0.0)	2(100.0)	11(100.0)	0(0.0) ***
Sorex trowbridgii	75(80.6)	18(19.4) **	89(49.7)	90(50.3)	198(70.5)	83(29.5) ***
Neurotrichus gibbsii	14(36.4)	8(63.6)	11(68.8)	5(31.2)	9(69.2)	4(30.8)
Scapanus orarius	1(11.1)	8(88.9) ***	7(61.1)	11(38.9)	18(75.0)	6(25.0) *
Order Rodentia						
Tamias townsendii	199(73.4)	72(26.6) *	365(49.4)	374(50.6)	872(44.0)	1110(56.0) ***
Spermophilus beecheyi					0(0.0)	1(100.0)
Tamiasciurus douglasii	1(50.0)	1(50.0)	0(0.0)	1(100.0)	3(60.0)	2(40.0)
Glaucomys sabrinus	18(85.7)	3(14.3)	8(36.4)	14(63.6)	88(67.7)	42(32.3) ***

Table 3.--(cont., p.2)

Species	1981		1982		1983	
	Removal	Control	Removal	Control	Removal	Control
Order Rodentia (cont.)						
Peromyscus maniculatus	806(67.0)	397(33.0)	286(40.7)	417(59.3) ***	535(14.9)	3061(85.1) ***
Neotoma cinerea	5(100.0)	0(0.0)	10(100.0)	0(0.0) **	2(100.0)	0(0.0)
Clethrionomys californicus	81(65.3)	43(34.7)	64(22.5)	221(77.5) ***	105(46.0)	123(54.0)
Arborimus albipes					1(100.0)	0(0.0)
Microtus oregoni	40(49.4)	39(50.6) **	29(23.8)	93(76.2) ***	104(49.8)	105(50.2)
Microtus richardsoni	5(100.0)	0(0.0)	27(96.4)	1(3.6) ***	54(38.6)	86(61.4) **
Zapus trinotatus	11(45.8)	13(54.2) *	181(56.7)	138(43.3) *	183(65.4)	97(34.6) ***
Order Carnivora						
Mustela erminea	2(50.0)	2(50.0)	0(0.0)	7(100.0) **	7(25.9)	20(74.1) *
Mustela frenata	1(100.0)	0(0.0)			4(100.0)	0(0.0) *

Chapter III

Table 4.--Mean ($\bar{X}$) and standard error (S.E.) for number of captures per utilized trap station on removal vs. control grids. T tests were used to document significant differences between removal and control grids (Bonferroni *$P<0.05$, using three comparisons).

Species	1981						1982						1983					
	Removal			Control			Removal			Control			Removal			Control		
	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.	n	$\bar{X}$	S.E.
Order Insectivora																		
Sorex vagrans	3	1.0	0.00															
Sorex monticolus	30	1.2	0.10	27	1.1	0.05	37	1.5	0.13	58	1.7	0.17	67	1.8	0.14	53	1.3	0.10
Sorex palustris										2	1.0	0.00						
Sorex bendirii										1	2.0		10	1.1	0.10			
Sorex trowbridgii	54	1.4	0.10	15	1.2	0.14	61	1.5	0.10	55	1.6	0.16	102	1.9	0.15	65	1.3	0.07 *
Neurotrichus gibbsii	13	1.1	0.08	8	1.0	0.00	11	1.0	0.00	5	1.0	0.00	7	1.3	0.18	3	1.3	0.33
Scapanus orarius	1	1.0		8	1.0	0.00	6	1.2	0.17	9	1.2	0.15	11	1.6	0.36	5	1.2	0.20
Order Rodentia																		
Tamias townsendii	117	1.7	0.09	44	1.6	0.14	169	2.2	0.11	166	2.3	0.11	223	3.9	0.19	243	4.6	0.24
Spermophilus beecheyi																1	1.0	
Tamiasciurus douglasii	1	1.0		1	1.0					1	1.0		3	1.0	0.00	2	1.0	0.00

Table 4.--(cont., p. 2)

Species	1981						1982						1983					
	Removal			Control			Removal			Control			Removal			Control		
	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
Order Rodentia (cont.)																		
Glaucomys sabrinus	17	1.1	0.06	3	1.0	0.00	8	1.0	0.00	12	1.2	0.11	66	1.3	0.08	35	1.2	0.10
Peromyscus maniculatus	187	4.3	0.25	97	4.1	0.29	107	2.7	0.27	101	4.1	0.35*	189	2.8	0.18	268	11.4	0.46 *
Neotoma cinerea	5	1.0	0.00				9	1.1	0.11				2	1.0	0.00			
Clethrionomys californicus	43	1.9	0.19	23	1.9	0.28	43	1.5	0.14	99	2.2	0.18*	46	2.3	0.23	69	1.8	0.12
Arborimus albipes													1	1.0				
Microtus oregoni	30	1.3	0.21	27	1.4	0.16	19	1.5	0.26	39	2.4	0.30	47	2.2	0.21	47	2.2	0.28
Microtus richardsoni	2	2.5	0.50				16	1.7	0.31	1	1.0		23	2.3	0.43	21	4.1	0.87
Zapus trinotatus	10	1.1	0.10	8	1.6	0.32	105	1.7	0.12	83	1.7	0.11	95	1.9	0.14	74	1.3	0.07 *
Order Carnivora																		
Mustela erminea	2	1.0	0.00	2	1.0	0.00				7	1.0	0.00	7	1.0	0.00	17	1.2	0.10
Mustela frenata	1	1.0											4	1.0	0.00			

Table 5.--Mean ($\bar{X}$) and standard error (S.E.) for number of captures per individual on removal vs. control grids. T tests were used to document significant differences between removal and control grids (Bonferroni *$P<0.05$, using three comparisons). Sample size is the number of individuals as given in Table 2.

	1981				1982				1983			
Species	Removal		Control		Removal		Control		Removal		Control	
	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.
Order Insectivora												
Sorex vagrans	1.0	0.00										
Sorex monticolus	1.1	0.07	1.2	0.10	1.3	0.13	1.4	0.10	1.2	0.06	1.0	0.03 *
Sorex palustris							1.0	0.00				
Sorex bendirii							1.0	0.00	1.0	0.00		
Sorex trowbridgii	1.1	0.04	1.0	0.00	1.0	0.02	1.1	0.03	1.1	0.02	1.1	0.04
Neurotrichus gibbsii	1.0	0.00	1.1	0.14	1.0	0.00	1.0	0.00	1.0	0.00	1.0	0.00
Scapanus orarius	1.0		1.1	0.14	1.8	0.48	1.6	0.43	2.2	0.65	2.0	0.58
Order Rodentia												
Tamias townsendii	3.6	0.53	3.6	0.80	5.5	0.61	3.9	0.43	8.1	0.80	7.3	0.60
Spermophilus beecheyi											1.0	
Tamiasciurus douglasii	1.0		1.0				1.0		1.5	0.50	2.0	
Glaucomys sabrinus	1.5	0.19	1.0	0.00	1.1	0.14	1.4	0.31	2.4	0.41	2.0	0.33

Table 5.--(cont., p. 2)

Species	1981				1982				1983				
	Removal		Control		Removal		Control		Removal		Control		
	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	
Order Rodentia (cont.)													
Peromyscus maniculatus	4.4	0.31	4.4	0.44	6.3	0.79	5.3	0.69	1.0	0.00	7.3	0.38	*
Neotoma cinerea	1.3	0.25			2.0	0.41			1.0	0.00			
Clethrionomys californicus	3.1	0.40	3.4	0.87	4.0	0.87	2.9	0.32	8.7	2.23	4.0	0.78	
Arborimus albipes									1.0				
Microtus oregoni	2.1	0.45	1.5	0.16	2.1	0.49	2.8	0.42	5.8	1.00	3.6	0.60	
Microtus richardsoni	5.0				3.0	0.71	1.0		5.4	2.37	10.8	3.63	
Zapus trinotatus	1.4	0.18	1.9	0.74	2.4	0.23	2.1	0.20	3.2	0.31	1.6	0.13	*
Order Carnivora													
Mustela erminea	1.0	0.00	1.0	0.00			1.0	0.00	1.0	0.00	1.2	0.10	
Mustela frenata	1.0								1.0	0.00			

Chapter III

Table 6.--Mean ($\bar{X}$) and standard error (S.E.) for number of stations utilized per individual on removal vs. control grids. T tests were used to document significant differences between removal and control grids (Bonferroni $^{*}P<0.05$, using three comparisons). Sample size is the number of individuals as given in Table 2.

Species	1981				1982				1983			
	Removal		Control		Removal		Control		Removal		Control	
	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.
Order Insectivora												
Sorex vagrans	1.0	0.00										
Sorex monticolus	1.1	0.07	1.2	0.10	1.3	0.12	1.4	0.09	1.2	0.05	1.0	0.03
Sorex palustris							1.0	0.00				
Sorex bendirii							1.0	0.00	1.0	0.00		
Sorex trowbridgii	1.0	0.03	1.0	0.00	1.0	0.02	1.1	0.03	1.1	0.02	1.1	0.04
Neurotrichus gibbsii	1.0	0.00	1.1	0.14	1.0	0.00	1.0	0.00	1.0	0.00	1.0	0.00
Scapanus orarius	1.0		1.1	0.14	1.5	0.29	1.4	0.30	1.4	0.18	1.7	0.33
Order Rodentia												
Tamias townsendii	3.4	0.44	3.2	0.69	4.8	0.50	3.3	0.32 *	6.0	0.54	5.3	0.39
Spermophilus beecheyi											1.0	
Tamiasciurus douglasii	1.0		1.0				1.0		1.5	0.50	2.0	
Glaucomys sabrinus	1.5	0.19	1.0	0.00	1.1	0.14	1.4	0.31	2.3	0.39	2.0	0.37

Table 6.--(cont., p. 2)

Species	1981				1982				1983			
	Removal		Control		Removal		Control		Removal		Control	
	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.
Order Rodentia (cont.)												
Peromyscus maniculatus	3.2	0.19	3.1	0.27	4.2	0.46	3.2	0.34	1.0	0.00	3.9	0.15 *
Neotoma cinerea	1.2	0.25			2.2	0.63			1.0	0.00		
Clethrionomys californicus	2.5	0.31	2.8	0.51	3.4	0.77	2.3	0.22	5.8	1.30	3.0	0.55
Arborimus albipes									1.0			
Microtus oregoni	1.9	0.29	1.4	0.16	1.8	0.30	2.0	0.22	4.3	0.71	2.6	0.35
Microtus richardsoni	2.0				2.7	0.60	1.0		2.8	0.76	4.2	1.05
Zapus trinotatus	1.4	0.18	1.3	0.29	2.3	0.22	2.1	0.20	3.0	0.27	1.6	0.13 *
Order Carnivora												
Mustela erminea	1.0	0.00	1.0	0.00			1.0	0.00	1.0	0.00	1.2	0.10
Mustela frenata	1.0								1.0	0.00		

Chapter III

Table 7.--Mean (X̄) and standard error (S.E.) for weight of adults on removal vs. control grids. T tests were used to document significant differences between removal and control grids (Bonferroni **P*<0.05, using three comparisons).

Species	1981						1982						1983					
	Removal			Control			Removal			Control			Removal			Control		
	n	X̄	S.E.	*n*	X̄	S.E.	*n*	X̄	S.E.	*n*	X̄	S.E.	*n*	X̄	S.E.	*n*	X̄	S.E.
Order Insectivora																		
Sorex vagrans	3	3.4	0.22															
Sorex monticolus	23	7.7	0.97	27	7.3	0.25	78	7.5	0.19	49	7.6	0.16	53	6.5	0.11	93	7.4	0.18 *
Sorex palustris										2	10.0	0.50						
Sorex bendirii										2	22.5	2.50	9	18.4	0.96			
Sorex trowbridgii	16	4.5	0.12	64	4.4	0.11	88	4.7	0.06	86	4.5	0.06	178	4.3	0.03	75	4.4	0.05
Neurotrichus gibbsii	14	8.9	0.20	7	7.9	0.50	11	8.0	0.35	5	8.2	0.27	9	8.0	0.20	4	7.9	0.12
Scapanus orarius	1	47.0		6	57.3	4.87	10	50.3	2.93	7	49.1	1.21	6	51.9	1.89	18	55.3	2.26
Order Rodentia																		
Tamias townsendii	71	77.2	0.70	192	78.0	0.61	365	75.9	0.34	356	78.7	0.46*	850	75.1	0.25	1092	78.4	0.24 *
Spermophilus beecheyi																1	387.0	
Tamiasciurus douglasii													3	180.7	10.97			
Glaucomys sabrinus	11	139.3	6.42	3	116.7	27.74	13	120.7	6.76	7	141.0	7.42	79	134.1	1.57	39	144.2	3.05 *

Table 7.--(cont., p. 2)

Species	1981						1982						1983					
	Removal			Control			Removal			Control			Removal			Control		
	n	X̄	S.E.	n	X̄	S.E.	n	X̄	S.E.	n	X̄	S.E.	n	X̄	S.E.	n	X̄	S.E.
Order Rodentia (cont.)																		
Peromyscus maniculatus	390	17.5	0.09	764	17.0	0.10*	399	20.2	0.24	276	18.1	0.15*	486	16.0	0.10	2880	17.3	0.07 *
Neotoma cinerea	2	270.8	70.75				3	201.7	31.67				1	178.0				
Clethrionomys californicus	80	24.3	0.46	42	22.5	0.64	208	22.2	0.44	63	22.3	0.27	105	24.6	0.41	119	21.9	0.33 *
Arborimus albipes													1	19.0				
Microtus oregoni	40	18.3	0.48	36	17.3	0.41	88	18.4	0.57	29	17.8	0.35	101	18.7	0.32	104	18.8	0.45
Microtus richardsoni	5	80.0	5.57				17	70.3	3.72	1	85.0		48	87.3	2.32	80	88.7	1.74
Zapus trinotatus	10	24.8	1.34	12	22.9	1.48	133	26.6	0.44	166	24.1	0.37*	178	26.9	0.35	96	27.0	0.50
Order Carnivora																		
Mustela erminea	2	55.3	10.25	1	70.0					4	52.9	8.96	3	73.0	1.53	8	56.5	6.44
Mustela frenata										1	100.0							

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