USE OF RIPARIAN AND UPLAND HABITATS BY SMALL MAMMALS

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ABSTRACT.—Mark-recapture was conducted from 1981 through 1983 in the Cascade Range of Oregon to examine the use of riparian and upland habitats by small mammals. Both number of individuals and species richness were greater in riparian than in upland areas. Because of the occurrence of several less-commonly captured species in riparian locations, species evenness was greatest in the upland. Among Insectivora, *Sorex monticolus* and *S. trowbridgii* were captured most often on riparian sites. Among insectivores adult males weighed more in riparian zones. Three rodents (*Peromyscus maniculatus*, *Microtus oregoni*, and *Zapus trinotatus*) were captured more frequently in riparian habitats; two rodents (*Tamias townsendii* and *Clethrionomys californicus*) were captured more frequently in upland habitats. Among all rodents, except *Z. trinotatus*, adult males weighed more in riparian areas. *Mustela erminea* was captured more frequently in riparian sites. Eight species had greater numbers of adults in breeding condition in riparian than in upland habitats. Conversely, six species had greater numbers of juveniles in the upland. Data from several species, including *T. townsendii*, *P. maniculatus*, *Z. trinotatus*, and *Glaucomys sabrinus*, indicated that riparian habitats act as a species source and upland areas act as a dispersal sink.

Relatively little is known about use of riparian habitats by terrestrial vertebrates within montane environments. Riparian research has focused on arid regions of the United States and, to some extent, on floodplains of low gradient streams and rivers (Johnson and Jones, 1977; Sands, 1977). Results of these studies are difficult to extrapolate to areas of the Pacific Northwest because high precipitation results in riparian vegetation much less distinct from adjacent areas. Riparian-related research in montane areas of the Pacific Northwest has focused on streamside vegetation and its influence on the aquatic ecosystem, with particular emphasis on fish habitats (Meehan et al., 1977; Swanson et al., 1976). Even in low-gradient floodplains and arid regions, most research has focused on the avian community (Austin, 1970; Carothers et al., 1974; Gaines, 1974; Stamp, 1978; Stauffer and Best, 1980). Few comprehensive studies of riparian small-mammal communities have been conducted (Boeer and Schmidly, 1977).

The purpose of this study was to test the hypothesis that riparian environments provide superior habitat for small mammals in montane areas. To investigate this hypothesis, I evaluated differences between habitats on the following criteria: species richness and abundance, number of breeding adults, number of juveniles, weight of adult males, and patterns of microhabitat selection. Reproductive characteristics and physical conditions were investigated because density alone may be misleading for assessing habitat quality (Van Horne, 1983). Unless these characteristics are considered, information may not be sufficient to distinguish source habitats (those responsible for the majority of juvenile production) and dispersal sinks (receiving areas for surplus individuals—Lidicker, 1975; Van Horne, 1983).

METHODS

Field research was conducted in the Cascade Range near Blue River, Oregon, approximately 75 km E Eugene. This area is charcterized by well-defined drainages and steep slopes. Annual precipitation ranges from 230 to 280 cm, 90% of which falls between October and April; temperatures are moderate with a mean July maximum of 29°C and mean January minimum of −3°C (Franklin and Dyrness, 1971). Soil and bedrock were described by Franklin and Dyrness (1971).

Trapping was conducted along Lookout Creek (two sites) on the H. J. Andrews Experimental Forest (T15S, R5E), along Hagan Creek in the Hagan Research Natural Area (T16S, R3E), and along Marten Creek in the Eugene District of the Bureau of Land Management (T17S, R3E). The Lookout Creek sites are old-growth stands, approximately 250 years old. The sites at Hagan and Marten Creeks are mature forest stands, approximately 100 years old.

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

Trapping was conducted June–November 1981–1983. Two trapping grids were established at each site, one in riparian and one in upland habitat. In 1981, each grid consisted of 56 trap stations spaced at 10-m intervals. In 1982 and 1983, grids were expanded to 70 trap stations. One Sherman trap (8 by 9 by 23 cm) was placed within 1 m of each grid coordinate and baited with whole oats and sunflower seeds. Each trap session lasted 4–9 days, for a total trap effort of 40,152 trap nights. Information recorded at the time of capture included species, sex, age class, weight, and reproductive condition. Animals were marked individually by toe clipping before release at the capture sites.

Habitat variables surveyed were selected on the basis of suspected relevance to small-mammal distributions. Trees and logs were surveyed in a square 100-m^2 area centered on each trap. Tree measurements included density, canopy cover by species, and canopy cover of deciduous and evergreen trees. Logs were measured for length and diameter and were classified according to a five-class decay scale (Franklin et al., 1981), in which the higher value represents more heavily decayed logs.

Herbs and shrubs were sampled in a square 9-m^2 area centered on each trap. Percent cover was recorded for each species and vegetative stratum. Percent cover of deciduous and evergreen trees, shrubs, and herbs was measured. Vegetative strata were classified as trees (>5 m), tall shrubs (2–5 m), small shrubs (0.5–2 m), tall herbs (30–50 cm), small herbs (5–30 cm), moss and lichen (<5 cm). Species richness of plants and percent of exposed soil and rock, leaf litter, moss, and lichen also were determined. On the upper Lookout Creek site, thermographs recorded meteorological data on the riparian and upland grids.

Species composition of small mammals, and number of juveniles and breeding adults were assessed by χ^2 analysis of capture frequencies among habitat types. Differences in weights of adult males between riparian and upland habitats were determined by t tests. Correlations between habitat variables and the number of captures at each trap station were tested by Spearman's rank-correlation coefficients (Sokal and Rohlf, 1981) to evaluate patterns of microhabitat selection. Correlations were considered significant at the $P < 0.005$ level. Pielou's index (J') was used as a measure of evenness (Pielou, 1966). Statistical comparisons of evenness between habitats were performed with a t test. Species richness was calculated as the number of small-mammal species captured in a specific habitat per year. Differences between habitats in percent ground cover, number of vegetative strata, and tree species were evaluated by t tests. Chi-square tests were used to analyze differences between habitats in abundance of tree species.

Results

Percent cover of deciduous herbs, shrubs, and trees, and of evergreen herbs was greater in riparian than in upland areas (Table 1). Conversely, percent cover of evergreen shrubs and trees was greater in the upland as was percent ground cover of moss. Because riparian sites included a portion of stream bed, percent of exposed rock was greater than in upland habitats.

On riparian grids, the most frequent herbaceous species were Oregon oxalis, western swordfern, and starry solomon plume (*Smilacina stellata*). Predominant shrubs were trailing blackberry (*Rubus ursinus*), red huckleberry (*Vaccinium parvifolium*), and California hazel (*Corylus cornuta*). Deciduous tree species, including big-leaf maple, vine maple, and red alder, were more abundant in riparian than in upland habitats (Table 2). The most abundant conifers in riparian areas were Douglas-fir and western hemlock.

On upland grids, twin flower (*Linnaea borealis*) was the most frequent herbaceous species, followed by bracken fern (*Pteridium aquilinum*) and starry solomon plume. Predominant shrubs were salal, Pacific rhododendron (*Rhododendron macrophyllum*), trailing blackberry, and Oregon grape. The conifers, Douglas-fir and western hemlock, occurred frequently, but hardwood species were sparse. Maximum air temperature and absolute range of air temperature both were consistently higher on upland sites.

Small mammals totaling 2,313 individuals were captured 9,382 times throughout the study.

TABLE 1.—*Mean* (±SE) *percent cover of vegetative strata and ground cover by habitat* (n = *280*), *analyzed by* t *tests for differences, near Blue River, Oregon, 1981–1983.*

Vegetative strata	Mean percent cover	
	Riparian	Upland
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
Trees (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
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

* $P < 0.01$.
** $P < 0.001$.

Although 19 species were trapped, data analysis was restricted to the 10 species for which >25 individuals were captured (except for calculations of species richness and evenness). Because species react differently to traps, information on relative abundance was used for comparison of abundances within species among habitats, and not among species within habitats.

Species richness of small mammals was greater in riparian than in upland sites in 1981 and 1982 (16 species in riparian habitats both years as opposed to 13 and 12 species in upland habitats in the 2 years, respectively) and equivalent in 1983 (12 species per habitat). In all 3 years, the total number of individuals was approximately 1.5 times greater in riparian areas ($P < 0.001$). Conversely, species evenness was greater in upland locations, although these differences were significant only during 1981. In 1981, the evenness index (±*SE*) for riparian habitats was 0.63 ± 0.04 and 0.79 ± 0.03 ($P < 0.03$) for riparian habitats; in 1982, the index was 0.63 ± 0.03 and 0.66 ± 0.04 for the two areas, respectively; and in 1983, the values were 0.80 ± 0.02 and 0.84 ± 0.02, respectively.

The order Insectivora was represented by *Sorex trowbridgii*, Trowbridge's shrew (331 individuals), *S. monticolus*, dusky shrew (226 individuals), and *Neurotrichus gibbsii*, shrew-mole (41 individuals). *S. trowbridgii* and *S. monticolus* were captured most often at riparian sites (*P*

TABLE 2.—*Mean* (±SE) *percent cover and percent frequency of abundant tree species by habitat* (n = *280*), *analyzed by* t *tests for differences, near Blue River, Oregon, 1981–1983.*

Tree species	Mean percent cover		Percent frequency	
	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

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

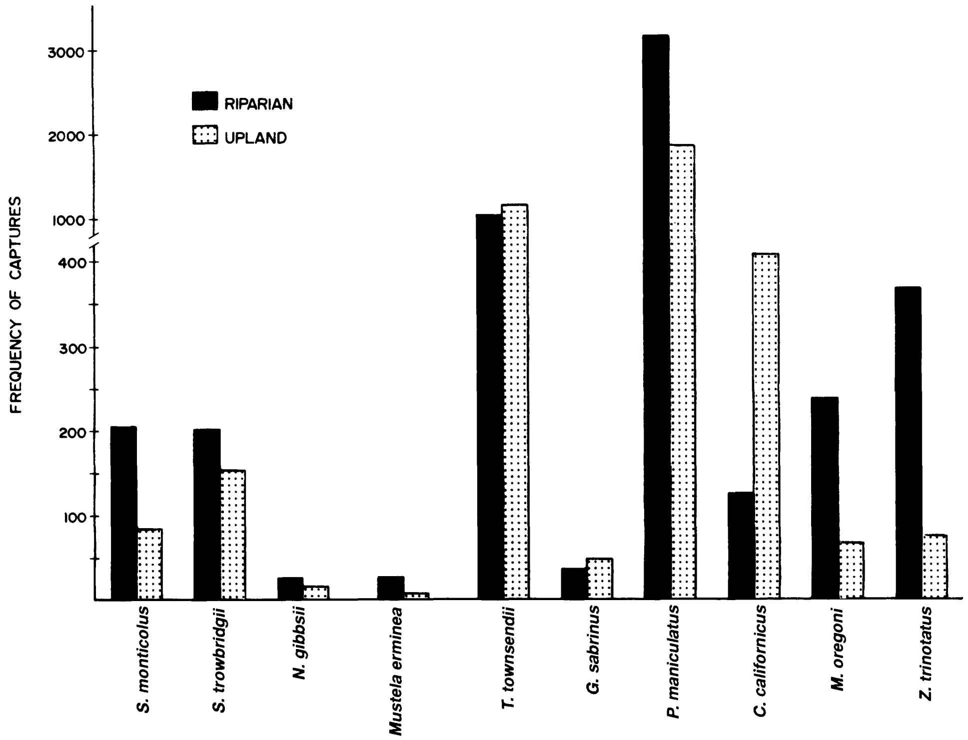

FIG. 1.—Frequency of captures of species by habitat type, near Blue River, Oregon, 1981–1983. Trap effort was equivalent in riparian and upland habitats.

< 0.05; Fig. 1). Although *N. gibbsii* was captured approximately 1.6 times more frequently in riparian than in upland areas, the differences were not significant. Among Rodentia, the most frequently captured species was the deer mouse, *Peromyscus maniculatus*. With 771 individuals, it represented 34.2% of the total number of animals caught. Other rodents captured included *Microtus oregoni*, creeping vole (116 individuals), *Zapus trinotatus*, Pacific jumping mouse (194 individuals), *Clethrionomys californicus*, western red-backed vole (152 individuals), *Tamias townsendii*, Townsend's chipmunk (343 individuals), and *Glaucomys sabrinus*, northern flying squirrel (52 individuals). *P. maniculatus*, *M. oregoni*, and *Z. trinotatus* were captured more frequently in riparian habitats than in upland habitats ($P < 0.001$); *T. townsendii* and *C. californicus* were captured more frequently in upland habitats ($P < 0.05$). For *G. sabrinus* the number of captures was virtually equivalent on riparian and upland sites. Among Carnivora, 28 *Mustela erminea*, ermine, were captured. *M. erminea* was captured more often in riparian locations ($P < 0.001$).

Among rodents a larger proportion of adult males were in breeding condition in riparian than in upland areas (Fig. 2). Although the trends were clear, the differences were not significant except for *T. townsendii* and *P. maniculatus*. In addition, a greater proportion of adult females were in breeding condition in riparian areas (Fig. 2). These values were significant for *T. townsendii*, *P. maniculatus*, and *C. californicus*. Among *S. monticolus* and *S. trowbridgii* a larger percent of males were in breeding condition in riparian habitats, but a larger percent of females were in breeding condition in upland habitats (Fig. 2). A greater proportion of *N. gibbsii* females were reproductively active in riparian areas, but an equivalent proportion of males in riparian and upland habitats were reproductively active. For *M. erminea*, the percent females in breeding condition was greatest in riparian habitats; no reproductively active males were found in either habitat type.

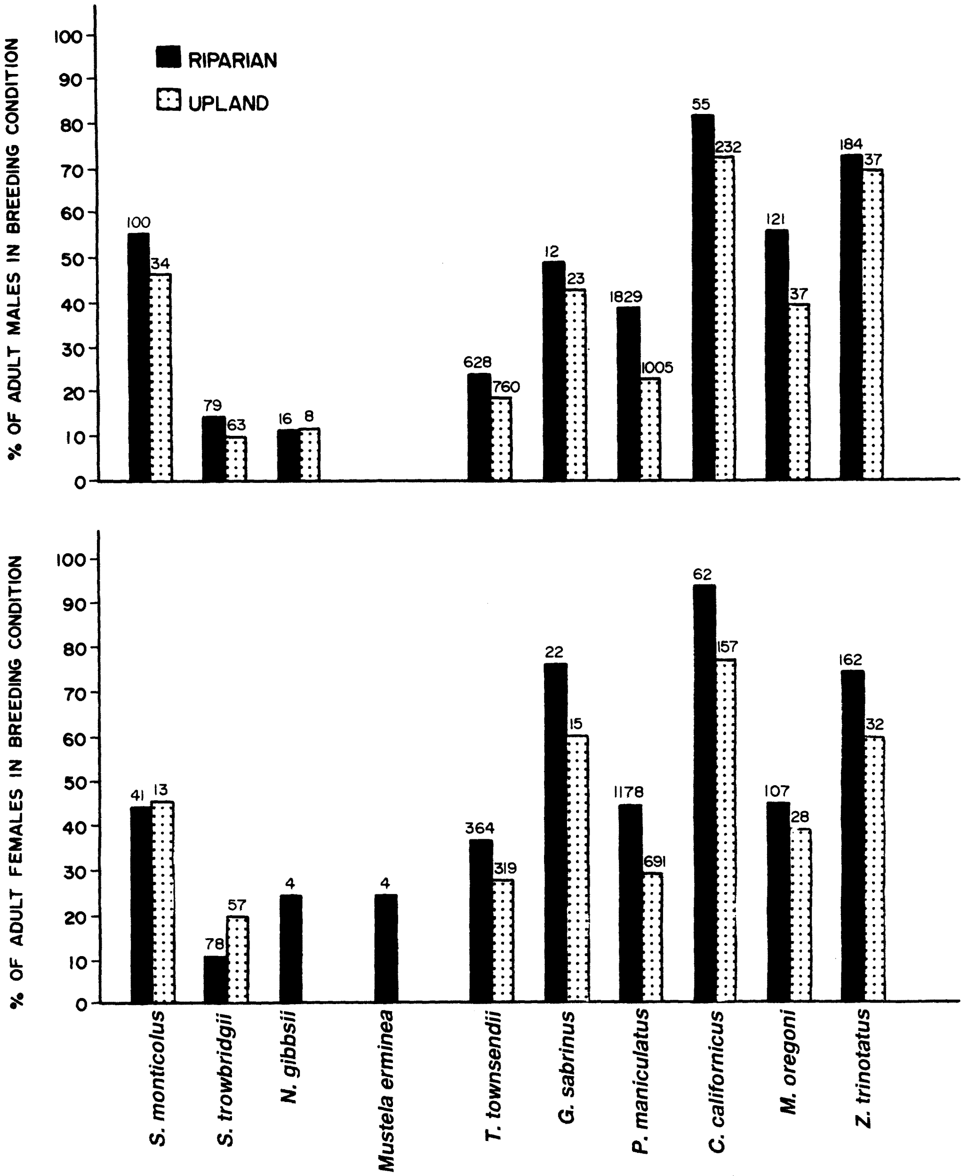

FIG. 2.—Percent of adult males and females in breeding condition by habitat types, near Blue River, Oregon, 1981–1983. Values above bars represent number of observations.

Juveniles were more prevalent in upland than in riparian sites for *S. monticolus* and *S. trowbridgii*; the reverse was true for *N. gibbsii* (Table 3). Among rodents, juvenile *T. townsendii*, *G. sabrinus*, *P. maniculatus*, and *Z. trinotatus* were more prevalent in upland habitats. The proportion of juveniles in the population was higher in riparian than upland locations for *C. californicus* and equivalent for the two habitat types for *M. oregoni* (Table 3).

Mean weight of adult males was used as an indicator of habitat quality (Van Horne, 1982*a*). Among insectivores adult males weighed more in riparian areas (Table 3). In addition, among all rodents except *Z. trinotatus*, adult males weighed more in riparian locations. Although these

TABLE 3.—*Mean (±SE) weights of adult males, and number and percent of juveniles by species and habitat type, near Blue River, Oregon, 1981–1983. Student's* t *tests were used to evaluate differences in weights between riparian and upland habitats* (n = 2). *Chi-square tests were used to evaluate differences in number of juveniles between habitats.*

Species	Weights of adult males (g)		Juveniles			
			Riparian		Upland	
	Riparian	Upland	*n*	Percent	*n*	Percent
Order Insectivora						
Sorex monticolus	7.21 ± 0.33	7.04 ± 0.27	203	17.7	83	24.1
Sorex trowbridgii	4.53 ± 0.08	4.46 ± 0.10	201	6.5	154	11.7
Neurotrichus gibbsii	8.11 ± 0.40	8.09 ± 0.39	21	3.8	16	0.0
Order Rodentia						
Tamias townsendii	77.68 ± 1.01	76.58 ± 0.94	1,014	1.9	1,106	2.3
Glaucomys sabrinus	137.39 ± 3.83	122.97 ± 6.95	36	5.6	49	20.4
Peromyscus maniculatus	17.55 ± 0.31	17.38 ± 0.26	3,140	4.2*	1,827	7.1
Cleithrionomys californicus	22.56 ± 0.97	22.38 ± 0.42	124	5.6	408	3.7
Microtus oregoni	18.91 ± 0.58	18.43 ± 0.53	238	2.9	68	2.9
Zapus trinotatus	23.97 ± 0.82	25.01 ± 1.49	365	4.7	75	8.0
Order Carnivora						
Mustela erminea	73.13 ± 1.20		1	52.0	6	50.0

* $P < 0.001$.

differences were not statistically significant they indicate a trend toward greater weights of adult males in riparian habitats. Correlations between habitat variables and the number of captures at each trap station were used to evaluate patterns of microhabitat selection (Table 4).

DISCUSSION

Both species richness and total number of individuals were greater in riparian areas than in upland areas. Most of the small-mammal species, including *S. monticolus*, *S. trowbridgii*, *P. maniculatus*, *M. oregoni*, *Z. trinotatus*, and *Mustela erminea*, were captured significantly more frequently in riparian than in upland areas. Only *T. townsendii* and *C. californicus* were captured significantly more often in upland areas. Most species also weighed more and included a greater number of adults in breeding condition in riparian habitats. These data indicate that riparian environments in montane areas provide superior habitat for several species of small mammals.

Superiority of the riparian areas may be based on factors including greater availability of water and greater availability of forage, such as fruits (especially *Vaccinium*), herbs, deciduous shrubs, and mast. Populations of invertebrates are more dense in streamside zones (Borror et al., 1981) providing greater food availability to insectivores. Thermograph data indicated that temperatures were lower and more stable in riparian than upland habitats, which could facilitate reduced energy expenditure in thermal regulation (Krebs, 1978). Soils in riparian areas generally are coarse in texture and more friable than in upland areas (Roberts et al., 1977), facilitating burrowing by small mammals.

Evenness was greater in upland habitats, indicating that numbers of individuals per species were more equally distributed there. The presence of several less-commonly captured species in riparian zones (e.g., *S. bendirii*, *S. palustris*, and *Mustela frenata* were never captured in the upland areas) and the high number of captures of *P. maniculatus* in riparian zones contributed to the unevenness of species distributions. All species captured in upland locations also were captured in riparian areas; however, several species were captured exclusively in riparian habitats.

With respect to patterns of microhabitat use, Ingles (1965:95) reported that *S. monticolus* occupies microhabitats "overgrown thickly with willows and tall sedges," suggesting a positive association with thick vegetative cover. Although these plant species were not present in substantial quantities on my study areas, the data support the association of *S. monticolus* with thick

TABLE 4.—*Correlations between habitat variables and number of captures at each trap* (n = 560), *near Blue River, Oregon, 1981–1983. Values are significant Spearman's rank-correlation coefficients.*

Species	Plant species richness	Decayed logs	Snag density	Lichen	Deciduous herbs	Evergreen herbs	Deciduous shrubs	Evergreen shrubs	Deciduous trees	Evergreen trees
Order Insectivora										
Sorex monticolus				−0.13*	0.17**	0.13*		−0.24**	0.16*	−0.16**
Sorex trowbridgii				−0.15*				−0.12*	0.16**	
Neurotrichus gibbsii			−0.13*	−0.12*						
Order Rodentia										
Tamias townsendii		0.21**	0.25**	0.29**	−0.12*	0.14*		0.15*	−0.31**	0.17**
Glaucomys sabrinus					−0.17**			0.17**	−0.17**	0.15*
Peromyscus maniculatus	0.32**	0.13*		0.19**	0.23**		0.19**	−0.31**		
Clethrionomys californicus			0.12*	0.22**				0.25**	−0.36**	0.25**
Microtus oregoni					0.31**	0.14*	0.16**	−0.20**		
Zapus trinotatus	0.28**				0.29**		0.27**	−0.27**	0.16**	−0.39**

* $P < 0.005$.
** $P < 0.0001$.

vegetative cover. *S. monticolus* was captured in sites with high percent cover of deciduous and evergreen herbs and deciduous trees. Abundance of *S. monticolus* was correlated negatively with evergreen shrubs and trees, and percent cover of lichen. Maguire (1983) reported that mesic areas with closed canopies rich in duff and decayed wood contribute to the primary microhabitats of *S. trowbridgii*. My study supports the association of *S. trowbridgii* with closed canopies, although abundance of *S. trowbridgii* was not correlated with highly decayed wood. *S. trowbridgii* occurred in sites dominated by deciduous trees, and that had a low percent cover of lichen and evergreen shrubs. *N. gibbsii*, a shallow burrower in soils rich in organic matter (Ingles, 1965), also is active on the surface of the ground (Whitaker et al., 1979). Although Whitaker et al. (1979) reported that *N. gibbsii* occurs in sites with large, highly decayed logs, correlations were not significant in my study with the total length of highly decayed logs. *N. gibbsii* occurred at sites with low cover of lichen and few snags.

Goodwin and Hungerford (1979) found a high correlation between density of *P. maniculatus* and cover of logs and stumps. In my study, *P. maniculatus* was captured most frequently in microhabitats with greater total length of heavily decayed logs (decomposition classes 3–5). Abundance of *P. maniculatus* also was correlated with greater species richness of plants and percent cover of lichen, deciduous herbs, and shrubs, and low percent cover of evergreen shrubs. Tevis (1956) reported that members of *T. townsendii* increase with greater quantities of herbaceous and shrubby vegetation. I found that *T. townsendii* occurred at sites with greater cover of evergreen herbs, shrubs, and trees. Abundance also was correlated with the woody component of the environment, specifically, number of snags and total length of highly decayed logs. In addition, *T. townsendii* was captured most often in sites with a high percent cover of lichen and low cover of deciduous herbs and trees.

The association of *M. oregoni* with riparian habitats (Dyrness, 1965; Gashwiler, 1972) probably relates to the extensive herbaceous and deciduous shrub cover in these habitat types. *M. oregoni* occurred in sites with high cover of herbs and deciduous shrubs and low cover of evergreen shrubs. Selection of microhabitats with greater amounts of herbaceous cover and deciduous shrubs probably reflects the diet of *M. oregoni*, which includes herbaceous vegetation, huckleberries, and hypogeous fungi (Maser et al., 1981). Abundance of *C. californicus* increased with increased number of snags possibly because dead wood contains high concentrations of mycorrhizae (Maser et al., 1978). *C. californicus* uses hypogeous fungi of the class Basidiomycetes as a source of food (Ure and Maser, 1982). When fungi becomes scarce, lichen is used for food. Lichen also is used for nest building (Ure and Maser, 1982). In my study, *C. californicus* occurred at sites with greater percent cover of lichen. Abundance also was correlated with greater percent cover of evergreen shrubs and trees and less cover of deciduous trees. The results of discriminant-function analysis indicate that microhabitat separation among these voles and *M. richardsonii* is significant and is a function of canopy cover of deciduous trees, percent cover of lichen, and distance from stream side (Doyle, 1987).

Mustela erminea is a wide-ranging species found in a variety of boreal habitats from agricultural lowlands, woodlands, and meadows to montane areas (Ingles, 1965; Svendsen, 1982). Abundance of *M. erminea* may be more directly tied to prey base than to specific vegetation variables (Svendsen, 1982). In my study, abundance of *M. erminea* was not significantly correlated with any of the environmental variables.

Data from several species in this study indicated that riparian habitats act as a species source and upland areas act as a dispersal sink. Dispersal sinks may develop if social interactions prevent subordinate 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 to which surplus individuals can disperse, and where survivorship and reproduction may be poor relative to that in 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 *P. maniculatus* in southeastern Alaska by Van Horne (1982*b*), who evaluated two different habitats for both adults and juveniles. Habitat densely populated by adults was characterized by high over-winter survival for both juveniles and adults. Conversely, habitat densely populated by juveniles was characterized by low over-winter survival for both juveniles and adults. In addition, weight of adult males was greater on the grid most densely populated by adults.

In my study, for *T. townsendii*, *G. sabrinus*, *P. maniculatus*, and *Z. trinotatus* upland habitats serve as a sink for juveniles dispersing from riparian habitats. These species have more juveniles in the upland areas in which the smaller adults (except *Z. trinotatus*) have reduced reproductive activity. Less suitable habitat (upland) may act as a sink for juveniles forced from suitable habitat (riparian) by aggressive adults.

Two species of insectivores also may follow this pattern. In *S. monticolus* and *S. trowbridgii*, the weight of adults and the number of reproductively active adult males was greater in riparian zones, whereas the number of juveniles and of reproductively active adult females was greater in upland areas. Reproductively active males may be dominant to both juveniles and adult females, thereby secure optimal habitat.

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